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Proceedings of the Sea Lamprey International Symposium

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In recognition of their contributions to our understanding of the sea lamprey, these proceedings are dedicated to:

John H. Howell,
Bernard R. Smith,
J. James Tibbles,
and the late Vernon C. Applegate.

En reconnaissance de leur contribution à notre compréhension de la lamproie marine, le présent procès-verbal est dédié à :

John H. Howell,
Bernard R. Smith,
J. James Tibbles
et le regretté Vernon C. Applegate.

Introduction to the Proceedings of the 1979 Sea Lamprey International Symposium (SLIS)[1]

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The Sea Lamprey International Symposium (SLIS) was the fifth in a series of symposia sponsored by the Great Lakes Fishery Commission. The sea lamprey control program, directed by the Commission, is one of the largest and most intensive efforts to control a vertebrate predator ever attempted. The program has met with significant success.

Sea lampreys are under a degree of control in the Great Lakes which, combined with present stocking practices, exploitation controls, and other programs, has produced a remarkable recovery of fishery resources. Comprehensive studies of the effects of lampricides on other organisms, terrestrial and aquatic, and in recent years a strict protocol of registration-oriented research proved that the chemical, when used by professional applicators, is environmentally safe. However, increasing costs, a single supplier of lampricides, and other considerations have caused concern.

As early as 1970, the Great Lakes Fishery Commission, obligated to continue to search for more efficient and economical methods to eradicate sea lampreys, encouraged the development of an integrated control program, including such suitable techniques as barrier dams, attractants and repellents, sterilization of one or both sexes, genetic manipulation, biological controls, and any other methods that could be developed and used in a compatible manner to reduce sea lamprey populations to levels below those causing economic or other damage.

In the belief that every program needs occasional close examination and can be improved, the Commission appointed a steering committee in 1975 to plan and implement a sea lamprey symposium. The main objectives of SLIS were threefold. First was the organization, consolidation, and publication of information on sea lamprey control and associated research. Second was to assemble experts in specialty areas involving lampreys to exchange knowledge and ideas to bring everyone to a common plateau of understanding, and finally to provide a forum for the participating scientists to develop new imaginative initiatives and stimulate new vigor in dealing with the effort to control sea lamprey predation and understand fish–lamprey interactions. With the firm conviction that the three objectives could be achieved and that many informative and valuable recommendations would be forthcoming, SLIS was held at Northern Michigan University, Marquette, Michigan, from July 30 to August 8, 1979.

The symposium was designed to be a workshop-type conference, and every attempt was made to provide a comfortable, informal atmosphere conducive to free interchange of information. Eighty-four participants from Australia, Canada, Denmark, England, Finland, Malaysia, Poland, Scotland, Sweden, and the United States assembled for 10 d and worked long and hard to ensure that the objectives of SLIS were met. The scientists were supported by an office staff of four very capable secretaries.

Three levels of synthesis were accomplished during the symposium. The first

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[1] This paper forms part of the Proceedings of the Sea Lamprey International Symposium (SLIS) convened at Northern Michigan University, Marquette, Michigan, July 30–August 8, 1979.

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level consisted of the discussion of the technical papers developed for SLIS. In themselves, these papers constituted an expression of the current understanding of the biology of lampreys, their interactions with fish populations, and methods for controlling sea lamprey abundance in the Great Lakes.

The second level of synthesis was the common objective of three task forces convened during the symposium. Everyone in attendance was arbitrarily assigned to one of the task forces. These groups were responsible for identifying the science necessary to further the understanding of lamprey ecology and for translating these notions into the operational terms necessary for delivery of an effective control program consistent with the objectives of an enhanced fish community in the Great Lakes. The three task forces were a Control Theory Task Force asked to address those hypotheses which relate to regulation of lamprey numbers; a Stock Effects Task Force assigned to examine hypotheses relating to the interactions between parasitic lampreys and their forage base; and an Assessment Measurements Task Force to investigate the question of sampling design, cost and precision with respect to the assessment of lamprey abundance, prey fish abundance, interactions between fish and lampreys, and the efficacy of control procedures.

The final level of synthesis was embodied in the efforts of an Optimization Committee. This group worked in parallel with the task forces, drawing together the inferences and conclusions necessary for the development of a set of options for presentation to the Great Lakes Fishery Commission.

The recommendations from the technical papers prepared for SLIS, the task force reports, inference papers, optimization committee report, and postsymposium correspondence were abstracted and presented to the Great Lakes Fishery Commission with the suggestion that a committee be selected to analyze and screen the recommendations, and then with Commission approval, submit these suggestions to the proper agencies for consideration and implementation. It was suggested also that a procedure for monitoring progress on the SLIS recommendations and reporting progress to the Commission be developed. Finally, the steering committee, believing that all the potential benefits could not be recognized in the short time allotted for the conference, recommended that some of the key people from SLIS should be reassembled in a year or two to review what took place, what has occurred in the interim, and perhaps suggest additional initiatives for sea lamprey control or management.

A brief outline of the SLIS agenda and these proceedings is as follows:

- Introduction
- Comparative Lamprey Biology
    - Lamprey Taxonomy
    - Biology and Life History
- The Sea Lamprey in the Great Lakes
    - History of Sea Lamprey Program
    - Effects of Control Measures on Lampreys and Other Aquatic Organisms
- Parasitic Lamprey Interactions with Fish Populations
    - Pacific and Atlantic Coasts of North America
    - Europe
    - Great Lakes and Connecting Waters
- Future of Integrated Control Methods for Sea Lamprey Control
- Models and Inferences
- Task Force Reports
    - Control Theory
    - Stock Effects
    - Assessment Measurements
- Optimization Committee Report

Acknowledgments

I must, in all fairness, express my appreciation not only to those who participated directly in SLIS, but to all others who provided support by accepting extra workloads at the institutions and agencies involved so that the attendees could expend their time and energy preparing their contributions.

I especially acknowledge the assistance and dedication of the other members of the steering committee: L. Olesen Larsen of Denmark; F. W. H. Beamish and W. J. Christie of Canada; and G. R. Spangler, A. K. Lamsa, B. J. McEachern, F. H. Dahl, and G. R. King of the USA. The committee formulated the program and selected the participants to be invited.

The contributions by chairmen of each section of the program and the task forces are gratefully acknowledged: J. H. Youson, I. C. Potter, R. J. Beamish, J. J. Tibbles, R. A. Braem, P. S. Maitland, A. H. Lawrie, R. Poff, G. R. Spangler, J. H. Howell, H. A. Regier, and C. J. Walters.

Assistance with the secretarial duties was given by Anna Little, Doreen Spiller, and Sally Specker.

With special gratitude I thank the wives who formed the "SLIS Sorority." Their presence and cheerful attitude added greatly to the social functions and helped to balance the predominantly male atmosphere.

Finally, without the encouragement, patience, and technical skills of Dr David G. Cook, Assistant Editor of the Journal, I do not believe that the printing of these proceedings would have been possible.

Why a Great Lakes Fishery Commission and Why a Sea Lamprey International Symposium[1]

CARLOS M. FETTEROLF JR.

Great Lakes Fishery Commission, Ann Arbor, MI 48105, USA

FETTEROLF, C. M. JR. 1980. Why a Great Lakes Fishery Commission and why a Sea Lamprey International Symposium. Can. J. Fish. Aquat. Sci. 37: 1588–1593.

Efforts to establish international fishery commissions and/or effective, complementary regulations and management programs for Great Lakes fisheries failed repeatedly from 1893 to 1952. By 1946 the sea lamprey (*Petromyzon marinus*), a parasitic predator native to the Atlantic Ocean, was established in the upper Great Lakes and recognized as an impending international catastrophe for the fisheries. This threat provided an added incentive to recast and complete earlier negotiations, and the Convention on Great Lakes Fisheries was entered into force in 1955. The Convention established the Great Lakes Fishery Commission to develop and coordinate fishery research programs, to advise governments on measures to improve the fisheries, and to develop measures and implement programs to control sea lamprey. Sea lamprey populations are currently at levels in all of the Great Lakes to allow acceptable survival and growth of desirable fish species. The commercial and recreational fisheries have revived to the point that their 1979 total economic impact is estimated at $1.16 billion. In 23 yr of operation the Commission has spent $54.5 million for sea lamprey control and research and feels a strong obligation to continue seeking more efficient and cost-effective management techniques. To produce a synthesis of opinion and recommendations for consideration in its future plans the Commission sponsored the Sea Lamprey International Symposium.

Key words: sea lamprey, Great Lakes, Great Lakes Fishery Commission, Sea Lamprey International Symposium, international agreements, international organizations

FETTEROLF, C. M. JR. 1980. Why a Great Lakes Fishery Commission and why a Sea Lamprey International Symposium. Can. J. Fish. Aquat. Sci. 37: 1588–1593.

À plusieurs reprises, entre 1893 et 1952, les efforts en vue de mettre sur pied des commissions internationales de pêche et/ou des réglementations complémentaires effectives pour les programmes de gestion des pêches des Grands Lacs se sont soldés par des échecs. Dès 1946, la grande lamproie marine (*Petromyzon marinus*), un prédateur parasite indigène de l'océan Atlantique, s'établissait dans la région supérieure des Grands Lacs et fut reconnue comme catastrophe internationale imminente pour les pêches. Cette menace fut un stimulant de plus à un retour sur les négociations antérieures et à leur conclusion. C'est ainsi que la Convention entre le Canada et les États-Unis relativement aux pêcheries des Grands Lacs entra en vigueur en 1955. Cette Convention mettait en place la Commission des pêcheries des Grands Lacs dans le but de développer et de coordonner les programmes de recherche sur les pêches, de conseiller les gouvernements sur les mesures à prendre pour améliorer ces pêches et mettre au point des mesures et exécuter des programmes visant à contrôler la grande lamproie marine. Les populations de grandes lamproies marines dans tous les Grands Lacs se trouvent présentement à des niveaux permettant une survie et une croissance acceptables des espèces de poissons désirables. Les pêches commerciales et récréatives se sont rétablies au point qu'on estime à 1,16 milliards de dollars leur impact économique total en 1979. Dans les 23 années de son existence, la Commission a dépensé 54,5 millions de dollars pour le contrôle de la grande lamproie marine et la recherche. Elle se sent fortement obligée de continuer à chercher des techniques de gestion plus efficaces par rapport aux coûts. C'est dans le but de produire une synthèse d'opinion et de recommandations pour considération dans ses plans futurs que la Commission a patronné le Colloque international sur la grande lamproie marine.

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THE Great Lakes Fishery Commission (GLFC) is charged by the governments of Canada and the United States to develop and coordinate fishery research programs, to advise governments on measures to improve the fisheries, and to develop measures and implement programs to control the sea lamprey (*Petromyzon marinus*) (Crowe 1975).

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[1] This paper forms part of the Proceedings of the Sea Lamprey International Symposium (SLIS) convened at Northern Michigan University, Marquette, Michigan, July 30–August 8, 1979.

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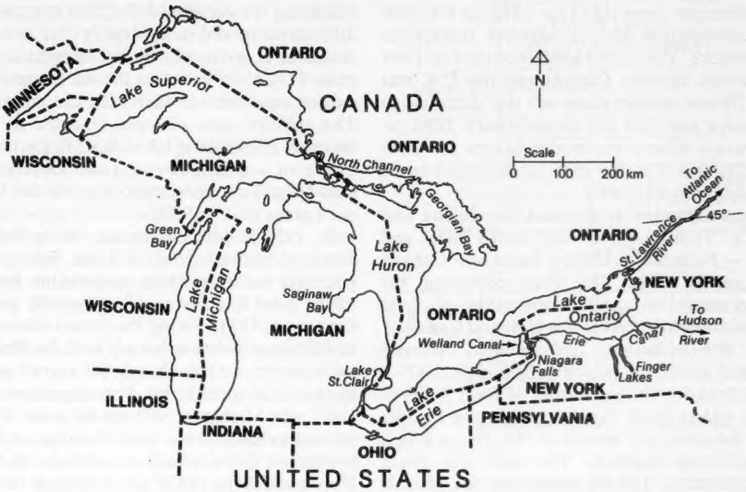
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WISCONSIN
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ONTARIO
Lake Ontario
To Hudson River
Welland Canal
Erie Canal
Niagara Falls
Finger Lakes
Lake St.Clair
NEW YORK
ILLINOIS
Lake Erie
PENNSYLVANIA
INDIANA
OHIO
UNITED STATES

FIG. 1. Fishery jurisdiction in the Great Lakes. The boundary between Ontario and various states is also the international boundary between Canada and the United States. The natural and man-made waterways between the lower lakes and the Atlantic Ocean are also shown.

Concurrent with development of sea lamprey control and other programs to rehabilitate the fisheries, there has been extensive work on lamprey biology, fish–lamprey interactions, and the socioeconomic impacts of sea lamprey predation and control. To provide an opportunity for experts to discuss these topics, synthesize findings, and recommend future direction, the Commission sponsored the Sea Lamprey International Symposium (SLIS) held at Northern Michigan University, Marquette, Michigan, USA, from July 30 through August 8, 1979. Many invitees and readers of the Proceedings will not be familiar with the circumstances which led to the establishment of the Commission or the need for the symposium. This introduction is intended to explain the raison d'être for both the GLFC and the SLIS.

Development of the Laurentian Great Lakes Basin since the early 1800s has had a major, continuing influence on the Great Lakes ecosystem and its fish populations. A wide range of activities including lumbering, farming, hydropower development, municipal and industrial waste disposal, canal construction, invasion by marine species, harbor and building site development, stocking of both exotic and native fish species, and intensive, species-selective fishing contributes to the many changes man has initiated in what was formerly a simple, slowly evolving flora and fauna (Baldwin et al. 1979; Berst and Spangler 1973; Christie 1973; Hartman 1973; Lawrie and Rahrer 1973; Smith 1972; Wells and McLain 1973).

Why a Great Lakes Fishery Commission

Management of the Great Lakes and the fishery resource is obviously complicated by the fact that the lakes are shared between Canada and the United States (Fig. 1). What is less obvious is that the fishery management and regulatory authority rests with the eight states whose borders include parts of the lakes, and with the Province of Ontario, whose border includes parts of four of the lakes. This situation is most complex on Lake Erie where the international boundary line runs the entire length of the lake, some 400 km. The Province of Ontario is responsible for managing and regulating the fishery in the northern half. Starting from the west, the States of Michigan, Ohio, Pennsylvania, and New York manage and regulate the fisheries in each of their waters in the southern half. This complexity and related situations on the other lakes have resulted in a series of efforts to develop effective, cooperative, management mechanisms.

There are several early reports of declines in Great Lakes fisheries. Decline of the Lake Ontario Atlantic salmon (*Salmo salar*) began as early as 1830 (Christie 1973). The report of the International Board of Inquiry for the Great Lakes Fisheries (Gallagher et al. 1943) states that by the early 1870s there was concern over decline of the fisheries in the contiguous waters of the U.S. and Canada and belief that there should be common action in regulating the fisheries. Efforts to develop appropriate mechanisms resulted in a series of unsuccessful attempts from 1893 to 1952 to establish joint fishery commissions and/or effective regulations of a uniform nature. The board explained that in 1893 a joint commission between Canada and the U.S. was appointed to foster preservation of the fisheries in contiguous waters and that the commission's 1896 report gave separate fishery recommendations for each Great Lake. The board stated that "these failed to be carried out," but did not say why.

In 1908 a proclamation announced the signing and ratification of a "Treaty between the United States and Great Britain — Fisheries in United States and Canada Waters" (Roosevelt 1908). The treaty concerned the "protection, preservation, and propagation of food fishes in the waters contiguous to the U.S. and Canada." Through this convention an International Fisheries Commission was appointed which prepared in 1909 a code of regulations for the protection of food fishes in 14 contiguous waters from the Atlantic to the Pacific, including the international waters of the Great Lakes and their connecting channels. The code was never brought into operation. The file card from the records of the Department of External Affairs Canada states that the treaty was terminated February 26, 1915 because of the failure of the U.S. Congress to approve the regulations.

In 1938 the Council of State Governments called international meetings of 60 state, federal, and provincial officials to consider how to bring into being effective, cooperative measures for the benefit of Great Lakes fisheries (Byrnes 1946). This led to establishment of an International Board of Inquiry for the Great Lakes Fisheries to study and report on the taking of fish, and to make recommendations "as to methods for preserving and developing" Great Lakes fisheries. The board reported in August 1942 and recommended joint action by the governments. Representatives of all concerned groups participated in drafting a "Convention between the United States of America and Canada for the Development, Protection, and Conservation of the Fisheries of the Great Lakes" which was signed by representatives of the United States and Canada on April 2, 1946. The major thrust of the Convention provided for the fixing of regulations by the Commission regarding seasons, open and closed waters, size limits, methods and effort, gear restrictions, stocking, introductions of species, and statistical records. By this time Great Lakes fisheries in general were entering a period of accelerating decline and the full significance of the sea lamprey was being recognized.

The sea lamprey can be a major factor in fish mortality. Native to the Atlantic Ocean, it feeds by attaching to other fish with its suctorial mouth and extracting body fluids. Although sea lamprey have had access to Lake Ontario via the St. Lawrence River for thousands of years, there is evidence they entered via the Erie Canal, opened to Lake Ontario in 1819 (Aron and Smith 1971). Christie (1973) discusses why the early chroniclers of the decline of Lake Ontario fisheries following the middle of the 19th century into the early 20th century did not identify the sea lamprey as a threat or contributing factor. It remained for Dymond et al. (1929) to state that the sea lamprey "undoubtedly causes considerable injury to the fishes of the lake." The authors' next sentence reported as high as 14 sea lamprey marks on a lake trout. For a discussion of the origin of sea lamprey in Lake Ontario and its entry into Lake Erie, most probably via the Welland Canal, see Lamsa et al. (1980).

In 1929 Hubbs and Brown wrote that the establishment of sea lamprey in Lake Erie added "another potential factor to those responsible for the depletion of the great fisheries of this extremely productive lake." Creaser (1932), noting the penetration of sea lamprey to Michigan rivers tributary to Lake Erie, stated, "The sea lamprey and the smelt (*Osmerus mordax*), which has recently spread over a great portion of Lake Huron and Lake Michigan, will act as great disturbers of the natural balance of the large fisheries of these extremely productive lakes, which are already in much distress." Hubbs and Pope (1937) in writing of the further spread through the Great Lakes stated that if the sea lamprey reached an abundance equal to or greater than that in Lake Ontario it "will add one more very serious factor to those already depleting the supply of lake trout, whitefish, suckers, catfish, and other commercial fishes in the Great Lakes." The forewarnings did not result in major, well-coordinated and adequately financed efforts to head off the sea lamprey, and by 1946 the exploding populations of sea lamprey in the upper lakes were recognized generally as an impending catastrophe for lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), and ciscoes (*Leucichthys* spp.), and to the commercial fishermen who made a living from these valuable species.

Despite the need for complementary regulations and management measures and the added threat of the sea lamprey, there was sufficient opposition to the transfer of authority from traditional regulatory bodies to an international body to prevent ratification of the 1946 Convention by the U.S. Congress. However, efforts to develop cooperative programs continued, and in that same year a Great Lakes Sea Lamprey Committee was established among the responsible federal, state, and provincial agencies to coordinate early research and control activities (Smith 1971).

Late in 1952 delegates from the two federal governments, the Province of Ontario, the Great Lakes states, and commercial fishing interests completed a draft for a new treaty, using the unratified 1946 treaty as a model. The delegates had past experience working on their side. They knew that granting regulatory power to a commission would be touchy and that the sea lamprey had to be reduced immediately by an international effort. The time was at last fully ripe for agreement, and on September 10, 1954 the Convention on Great Lakes Fisheries between the United States of America and Canada was signed by representatives of both countries, ratified in the U.S. on June 6, 1955, in Canada on October 6, 1955, and entered into force on October 11, 1955. By that time lake trout production from lakes Huron and Michigan was 99% lower than the average annual commercial catch during the 1930s.

Knowing the background it is predictable that the opening words of the Convention would be,

> *The Government of the United States of America and the Government of Canada,*
>
> *Taking note of the interrelation of fishery conservation problems and of the desirability of advancing fishery research in the Great Lakes,*
>
> *Being aware of the decline of some of the Great Lakes fisheries,*
>
> *Being concerned over the serious damage to some of these fisheries caused by the parasitic sea lamprey and the continuing threat which this lamprey constitutes for other fisheries,*
>
> *Recognizing that joint and coordinated efforts by the United States of America and Canada are essential in order to determine the need for and the type of measures which will make possible the maximum sustained productivity in Great Lakes fisheries of common concern have agreed as follows - - - -.*

In Article IV the Commission was assigned the following duties:

- *(a) To formulate a research program or programs designed to determine the need for measures to make possible the maximum sustained productivity of any stock of fish in the Convention Area which, in the opinion of the Commission, is of common concern to the fisheries of the United States of America and Canada and to determine what measures are best adapted for such purpose;*
- *(b) To coordinate research made pursuant to such programs and, if necessary to undertake such research itself;*
- *(c) To recommend appropriate measures to the Contracting Parties on the basis of the findings of such research programs;*
- *(d) To formulate and implement a comprehensive program for the purpose of eradicating or minimizing the sea lamprey populations in the Convention Area; and*
- *(e) To publish or authorize the publication of scientific and other information obtained by the Commission in the performance of its duties.*

Note that no rule-making responsibility was assigned.

ORGANIZATION OF THE COMMISSION

In the Convention the contracting parties agreed to establish the Great Lakes Fishery Commission composed of two national sections, each with one vote, and stipulated that a decision or recommendation of the Commission shall be made only with the approval of both Sections. Each national section consists of four persons knowledgeable from training or experience in natural resource administration or fisheries. Canadian commissioners are appointed by the Privy Council for renewable 2-yr terms. The four U.S. commissioners are appointed by the President to serve at the President's pleasure. The Commission, served by a six-person Secretariat, pursues much of its program through committee structure involving representatives of the agencies with mandates for fishery management and research, and the academic community (Fig. 2). Central committees include commissioners as members, technical committees do not. The Canadian Section may invite the participation of advisors as it sees fit. The U.S. Section is charged by law to appoint for each lake an advisory committee on which each bordering state may be represented by not more than four persons representing the commercial fishing industry, the sport fishery, the public-at-large, and state agencies having jurisdiction over fisheries.

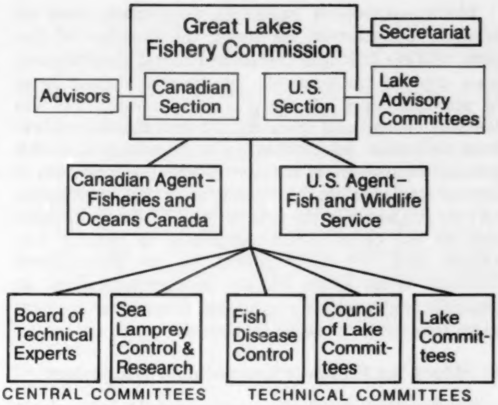
Great Lakes Fishery Commission
Secretariat
Advisors
Canadian Section
U.S. Section
Lake Advisory Committees
Canadian Agent–Fisheries and Oceans Canada
U.S. Agent–Fish and Wildlife Service
Board of Technical Experts
Sea Lamprey Control & Research
Fish Disease Control
Council of Lake Committees
Lake Committees
CENTRAL COMMITTEES
TECHNICAL COMMITTEES

FIG. 2. Organization chart of the Great Lakes Fishery Commission.

Since the Commission first assumed responsibility for the sea lamprey control and research program in 1955, it has entered into annual memoranda of agreement with the U.S. Fish and Wildlife Service and the Fisheries Research Board of Canada (now Fisheries and Oceans Canada) as its agents to carry out the operational phase. The most important control technique is the application of a chemical selectively toxic to lamprey to the tributaries in which larvae are developing. In fiscal years 1958 through 1980 the people of the United States and Canada have spent $54.5 million through the Commission for sea lamprey control and research. These funds have been provided 69% through the U.S. Department of State and 31% through Fisheries and Oceans Canada with the approval of External Affairs Canada. The 69:31 ratio was established on the basis of average annual Great Lakes commercial catches of lake trout before the impact of the sea lamprey.

The Commission's initiatives, undertaken with its principal cooperators, the states, the Province of Ontario, and the U.S. and Canadian Federal governments, have evolved consecutively into several related areas of activities, each of which is still ongoing: (1) sea lamprey control and research; (2) coordination of lake trout and other fish stocking; (3) coordination of fish population assessment and development of strategies to control exploitation; (4) registration of lampricides; (5) investigation of the feasibility of further rehabilitation of the Great Lakes ecosystem to reattain lost values; and (6) development of an international Strategic Great Lakes Fishery Management Plan, an umbrella under which operational fishery management plans for each lake can be developed.

Why a Sea Lamprey International Symposium

Sea lamprey populations are currently at levels in all of the Great Lakes to allow sufficient survival and growth of desirable species to produce valuable commercial and recreational fisheries. In the period following the collapse of predator populations and commercial fisheries, and when fish community structure was seriously disrupted, the Great Lakes sport fishery reached a low point and was important only in a few local areas. Continuing controls on sea lamprey have made possible the reestablishment of predators such as lake trout and steelhead (*Salmo gairdneri*) and the introduction of Pacific salmon (principally *Oncorhynchus kisutch* and *O. tshawytscha*) and splake (a hybrid between lake and brook trout, *Salvelinus fontinalis*) to bring the predator/prey ratio to a level similar to the pre-sea lamprey condition. The ratio is maintained by stocking hatchery raised fish and currently about 25 million salmon and trout fingerlings and yearlings are planted annually in the Great Lakes.

Development of the fishery has been spectacular. D. P. Talhelm et al. (Great Lakes Fish. Comm., Ann Arbor, MI, 1979, mimeograph), have provided some current estimates of Great Lakes fishery values and economic impact. About 24 million angler days of sport fishing for Great Lakes fish were estimated for 1979. Current annual expenditures for angling for Great Lakes fish are estimated at $440 million, about a quarter of which goes toward purchasing boats, motors, boat trailers, and related equipment for the purpose of angling. The total annual economic impact of Great Lakes angling is about $1 billion.

The landed value of Great Lakes commercial fish was about $25 million in 1979, with a total economic impact of about $160 million. The combined total economic impact of the recreational and commercial fisheries is about $1.16 billion annually. This compares with total management and rehabilitation costs of about $40 million annually.

The current value is a sign that the fishery and environmental management and research programs of the eight Great Lakes states, the Province of Ontario, the U.S. and Canadian Federal governments, the GLFC, and its sister commissions have been effective in rehabilitating the distressed ecosystems of the Great Lakes to a point. Much of the fishery management success to date has been bioengineered through sea lamprey control, artificial replenishment of native species by stocking, introduction of Pacific salmon, and application of knowledgeable regulations controlling harvest. The Commission's goal for the development and maintenance of balanced fish communities supported by natural reproduction is not yet attainable. Managers are handicapped by a variety of factors including contaminants in fish; insufficient natural reproduction by some species; loss of habitat quality and a continuing loss of habitat quantity; undesirable fish community structure in several areas; extinction of some species; loss of genetic strains; and inadequate laws for effective control of harvest in some situations.

Through continuing management, and the application of research findings to management, the value of the fisheries should continue to grow. To ensure continuing development of knowledge, synthesis of what is already known, and to ensure that the Commission and its cooperators are prepared to take advantage of the improving habitat quality as water management programs are implemented, the Commission promotes a series of symposia by active participation and varying degrees of financial and developmental support. These symposia include 1971, the international symposium on Salmonid Communities in Oligotrophic Lakes (SCOL) (J. Fish. Res. Board Can., Vol. 29, No. 6); 1972, Bio-Engineering Symposium for Fish Culture-I; 1976, the Percid International Symposium (PERCIS) (J. Fish. Res. Board Can., Vol. 34, No. 10); 1978, A Symposium on Selected Coolwater Fishes of North America (Kendall 1978); 1979, the Sea Lamprey International Symposium (SLIS) (Can. J. Fish. Aquat. Sci. Vol. 37, No. 11); 1979, Bio-Engineering Symposium for Fish Culture-II; and 1980, the Stock Concept Symposium (STOCS).

In 23 yr of operation the Commission has spent $54.5 million on sea lamprey control and research. Given current inflation rates, it is likely a similar amount will be spent in the next 7 or 8 yr. The Commission, feeling obligated not to rest on its laurels, but to continue seeking more efficient and cost-effective ways to control sea lamprey, took two progressive steps during 1975. The first was to request the Commission's Scientific Advisory Committee[2] to conduct a technical review of the sea lamprey control research program conducted at the Hammond Bay Biological Station, USFWS. The audit resulted in 30 recommendations related to ongoing and future research and control activities (Scientific Advisory Committee, GLFC, Great Lakes Fish. Comm., Ann Arbor, MI, 1975, mimeograph). The recommendations continue to have a significant influence on the program.

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[2] Name changed to Board of Technical Experts in 1979.

The second step occurred at the September 1975 GLFC Executive Meeting when a three-person Steering Committee of F. W. H. Beamish (Univ. of Guelph), Richard Pycha (USFWS), and Aarne Lamsa (GLFC Secretariat) was appointed and charged to develop a sea lamprey symposium. Basically, the Commission said it is time to take a good, hard look at sea lamprey control and research. Are we in a rut? What do we know? Are we using what we know? What don't we know and what should we know? Where do we go from here?

Later in the planning process for SLIS, Bernard R. Smith (USFWS) became chairman of the Steering Committee. We rephrased the above gut-level questions into a more sophisticated statement for use in the announcement, the "Purpose of SLIS is more than the obvious objectives of organization, consolidation, and publication of information on sea lamprey control and associated research. It is the Commission's desire that the experts in specialty areas involving lampreys bring each other up to a common plateau of understanding which will stimulate new thoughts and result in imaginative initiatives and renewed vigor in dealing with our long-standing effort to control sea lamprey predation and understand fish–lamprey interactions."

In essence, the Commission is playing its usual role. It is providing a forum and asking you, the sea lamprey control specialists, the resource managers, and the research scientists, how to optimize the sea lamprey control and research program which the Canadian and U.S. governments have charged the Commission to conduct.

I repeat what Commission Chairman Kenneth H. Loftus said in welcoming participants, that the Commission is very pleased with the planning and organization done by Chairman Bernie Smith and his Steering Committee, and is delighted that each of you could accept the invitation. The stage is now set and the actors are in place. Your recommendations are needed and they will be considered in future programs. The product of your efforts is eagerly anticipated with confidence that it will exceed the Commission's expectations.

Acknowledgments

I appreciate the constructive criticism of earlier drafts of this paper by F. E. J. Fry, Aarne K. Lamsa, Andrew H. Lawrie, Kenneth H. Loftus, Betty J. McEachern, Margaret A. Ross, Bernard R. Smith, Stanford H. Smith, and J. James Tibbles. These drafts went into greater detail on the efforts to establish joint commissions and regulations, the personalities involved, and my interpretation of the reasons for success or failure. GLFC Commissioner Loftus, former Commissioner Fry, and former GLFC Board of Technical Experts Chairman Lawrie agreed that this paper was not the proper vehicle for a detailed history but that the Commission should sponsor development of such a history in conjunction with its 25th anniversary year, 1980–81.

ARON, W. I., AND S. H. SMITH. 1971. Ship canals and aquatic ecosystems. Science 174: 13–20.

BALDWIN, N. S., R. W. SAALFELD, M. A. ROSS, AND H. J. BUETTNER. 1979. Commercial fish production in the Great Lakes 1897–1977. Great Lakes Fish. Comm. Tech. Rep. 3: 187 p.

BERST, A. H., AND G. R. SPANGLER. 1973. Lake Huron — the ecology of the fish community and man's effects on it. Great Lakes Fish. Comm. Tech. Rep. 21: 41 p.

BYRNES, J. F. 1946. Letter to the President. *In* Message from the President of the United States transmitting a convention between the United States of America and Canada for the development, protection, and conservation of the fisheries of the Great Lakes, signed at Washington, April 2, 1946. 79th Congress, 2d Session, Senate, Executive C, April 22, 1946, U.S. Govt. Printing Office, Washington, D.C. 11 p.

CHRISTIE, W. J. 1973. A review of the changes in the fish species composition of Lake Ontario. Great Lakes Fish. Comm. Tech. Rep. 23: 65 p.

CREASER, C. W. 1932. The lamprey *Petromyzon marinus* in Michigan. Copeia 1932 (3): 157.

CROWE, W. R. 1975. Great Lakes Fishery Commission History, Program, and Progress. Great Lakes Fish. Comm. 22 p.

DYMOND, J. R., J. L. HART, AND A. L. PRITCHARD. 1929. The fishes of the Canadian waters of Lake Ontario, p. 3–35. *In* Univ. of Toronto Studies, Biological Series No. 33. Publication No. 37 of the Ontario Fisheries Research Laboratory.

GALLAGHER, H. R., A. G. HUNTSMAN, D. J. TAYLOR, AND J. VAN OOSTEN. 1943. International Board of Inquiry for the Great Lakes Fisheries, Report and Supplement. U.S. Govt. Printing Office, Washington, D.C. 213 p.

HARTMAN, W. L. 1973. Effects of exploitation, environmental changes, and new species on the fish habitats and resources of Lake Erie. Great Lakes Fish. Comm. Tech. Rep. 22: 43 p.

HUBBS, C. L., AND D. E. S. BROWN. 1929. Materials for a distributional study of Ontario fishes. Trans. R. Can. Inst. 17: 56 p.

HUBBS, C. L., AND T. E. B. POPE. 1937. The spread of the sea lamprey through the Great Lakes. Trans. Am. Fish. Soc. 66: 172–176.

KENDALL, R. L. [ed.] 1978. Selected coolwater fishes of North America. American Fisheries Society, Washington, D.C. 437 p.

LAMSA, A. K., C. M. ROVAINEN, D. KOLENOSKY, AND L. H. HANSON. 1980. Sea lamprey (*Petromyzon marinus*) control — where to from here? Report of the SLIS Control Theory Task Force. Can. J. Fish. Aquat. Sci. 37: 2175–2192

LAWRIE, A. H., AND J. F. RAHRER. 1973. Lake Superior — a case history of the lake and its fisheries. Great Lakes Fish. Comm. Tech. Rep. 19: 69 p.

ROOSEVELT, T. 1908. Treaty between the United States and Great Britain — Fisheries in United States and Canada Waters. Treaty Series No. 498, U.S. Govt. Printing Office, Washington, D.C. 5 p.

SMITH, B. R. 1971. Sea lampreys in the Great Lakes of North America. p. 207–247. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. I. Academic Press, New York.

SMITH, S. H. 1972. Factors of ecologic succession in oligotrophic fish communities of the Laurentian Great Lakes. J. Fish. Res. Board Can. 29: 717–730.

WELLS, L., AND A. L. MCLAIN. 1973. Lake Michigan — Man's effects on native fish stocks and other biota. Great Lakes Fish. Comm. Tech. Rep. 20: 55 p.

Editor's Note

To reduce possible ambiguities to a minimum this Journal uses the scientific and common names of North American fishes recommended by the American Fisheries Society (R. M. Bailey, J. E. Fitch, E. S. Herald, E. A. Lachner, C. C. Lindsey, C. R. Robins, and W. B. Scott. 1970. A list of common and scientific names of fishes from the United States and Canada (3rd edition). Am. Fish. Soc. Spec. Publ. 6: 150 p.). However, lamprey nomenclature is in a state of flux, and the Journal does not wish to inhibit taxonomic debate by arbitrarily favoring one system over another. Therefore, in the taxonomic papers that follow, the authors have used names as they see fit with no editorial restrictions.

The two classical taxonomy papers presented at SLIS represent two rather divergent opinions. To balance these views and to provide input from the names committee of the American Fisheries Society we have invited a commentary on lamprey systematics from the chairman of this committee, Dr. R. M. Bailey. The Journal editors and SLIS officials thank Dr. Bailey for undertaking this difficult task.

D. G. Cook

The Petromyzoniformes with Particular Reference to Paired Species[1]

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Potter, I. C. 1980. The Petromyzoniformes with particular reference to paired species. Can. J. Fish. Aquat. Sci. 37: 1595–1615.

The distribution of living lampreys (Petromyzoniformes) is antitropical, a feature almost certainly related to the fact that the ultimate incipient lethal temperature of ammocoetes lies between ~28 and 32°C. In general, the species that attain the largest body size have the widest distribution. The holarctic species are placed in the Petromyzonidae, while those of the Southern Hemisphere are assigned either to the Geotriidae or Mordaciidae. Reference is made to the techniques used in lamprey systematics, placing particular emphasis on defining the terminology of the components of the dentition and the ways in which body proportions can be measured. Using dentitional characters, the Petromyzonidae can be arranged in a logical sequence from *Ichthyomyzon* and *Petromyzon* to either *Caspiomyzon* or to series consisting either of *Eudontomyzon* and *Tetrapleurodon* or the subgenera of *Lampetra*, i.e. *Entosphenus*, *Lethenteron*, and *Lampetra*. A list is given of the 17 parasitic and 22 nonparasitic lampreys described from the Northern and Southern hemispheres. The evolution of nonparasitic lampreys has involved an extension of larval life and a reduction in the postmetamorphic period, a process which has led to a marked reduction in the size of the mature adults. The more conspicuous differences between nonparasitic and parasitic species start to appear after the onset of metamorphosis. These include the rapid enlargement and maturation of gonads in nonparasitic species. However, significant differences have been found between the larvae of nonparasitic lampreys and those of their parasitic ancestor in such features as the number of oocytes, trunk myomeres, and size at the onset of metamorphosis.

Key words: lampreys, life cycles, parasitic, nonparasitic, distribution, dentition, phylogeny, Petromyzonidae, Geotriidae, Mordaciidae

Potter, I. C. 1980. The Petromyzoniformes with particular reference to paired species. Can. J. Fish. Aquat. Sci. 37: 1595–1615.

Les lamproies actuelles (Petromyzoniformes) ont une distribution antitropicale, une caractéristique presque certainement liée au fait que la température ultime de début des mortalités se situe entre 28 et 32°C environ. En général, les espèces qui atteignent les plus grandes tailles ont une aire plus étendue. Les espèces holarctiques sont classées parmi les Petromyzonidae, alors que celles de l'hémisphère sud sont classées soit parmi les Geotriidae ou les Mordaciidae. L'auteur mentionne les méthodes utilisées dans la systématique des lamproies, mettant l'accent sur la définition des termes des éléments de la dentition et sur les manières dont sont mesurées les proportions du corps. À partir des caractéristiques de la dentition, les Petromyzonidae peuvent être placés dans un ordre logique, depuis *Ichthyomyzon* et *Petromyzon* jusqu'à soit *Caspiomyzon* ou à des séries constituées par *Eudontomyzon* et *Tetrapleurodon* ou par les sous-genres de *Lampetra*, i.e. *Entosphenus*, *Lethenteron* et *Lampetra*. Le présent article contient une liste des 17 lamproies parasites et 22 non parasites décrites pour les hémisphères nord et sud. L'évolution des lamproies non parasites a comporté un prolongement de la vie larvaire et une réduction de la période postmétamorphique, processus qui a conduit à une diminution marquée de la taille des adultes matures. C'est après le début de la métamorphose que les différences les plus visibles entre les espèces parasites et non parasites commencent à se manifester. Parmi ces différences, on note le grossissement et la maturation rapides des gonades chez les espèces non parasites. Cependant, on a observé des différences significatives entre les larves de lamproies non parasites et celles de leurs ancêtres parasites dans certains caractères, tels que nombre d'ovocytes, myomères du tronc et taille au début de la métamorphose.

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The marked difference between the vertebrates without jaws and those with jaws has been considered so fundamental in terms of vertebrate evolution that many authorities have divided the subphylum Vertebrata (= Craniata) into two superclasses or branches, the Agnatha and Gnathostomata (Berg 1948; Young 1950). Although there was a relatively diverse agnathan fauna

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[1] This paper forms part of the Proceedings of the Sea Lamprey International Symposium (SLIS) convened at Northern Michigan University, Marquette, Michigan, July 30–August 8, 1979.

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during the midpalaeozoic, the only extant representatives of the group are the lampreys and the hagfishes. The presence of a round "mouth" in both of these latter groups has led some taxonomists to place these living jawless fishes in a single class, the Cyclostomata (Holly 1933). While this term is misleading in that it implies a greater affinity of the living forms than is justified (Berg 1940; Heintz 1963), it is probably worthwhile retaining the colloquial name cyclostome to cover the living jawless fishes.

In this paper I have outlined the factors affecting the distribution of the living lampreys (Petromyzoniformes) and described the characters used in the systematics of this group. This is followed by a proposal for phylogenetic relationships based primarily on lamprey dentition. A list of the Northern and Southern Hemisphere species and their distribution is also given. Finally, I have made comparisons between the members of paired species and drawn conclusions as to the trends that have occurred during the evolution of nonparasitic lampreys from their parasitic ancestors.

Factors Influencing the Distribution of the Petromyzoniformes

TEMPERATURE

Since lampreys, like the hagfishes, have an antitropical distribution (Hubbs 1952; Fontaine 1958; de Buen 1961; Adam and Strahan 1963; Hubbs and Potter 1971), temperature is almost certainly a major factor in restricting them to the cooler regions of the world. This view is consistent with the fact that, in general, lampreys are found northward and southward of the 20°C annual isotherm in the Northern and Southern Hemispheres, respectively (Lanzing 1957). A conspicuous exception to the above generalization is provided by the Mexican genus *Tetrapleurodon*. However, since the parasitic (*T. spadiceus*) and nonparasitic species (*T. geminis*) comprising this genus are confined to rivers and lakes at relatively high altitudes, they are not exposed to the type of temperature regime that would be found in coastal river systems at the same latitude (Álvarez del Villar 1966; Hubbs and Potter 1971).

Confirmation that temperature is the factor preventing the colonization of the warmer waters of the world has been provided by studies on lethal temperatures carried out on ammocoetes in the laboratory. Respective ultimate incipient lethal values of 29.2, 31.4, and 28.3°C have been recorded for *Lampetra planeri* and *Petromyzon marinus* of the Northern Hemisphere (Potter and Beamish 1975) and for *Geotria australis* of the Southern Hemisphere (Macey and Potter 1978). Lethal experiments carried out by Potter and Beamish (1975) on larval *Ichthyomyzon fossor* and *Lampetra lamottenii* acclimated only at 15°C indicate that the ultimate incipient lethal temperature of these Holarctic lampreys is similar to those of the three species given above. Preliminary experiments with *Mordacia mordax* have yielded similar results. Thus, since river systems in many of the warmer parts of the world are often warmer than 28°C for significant periods, it is the limited tolerance of the ammocoete to warm temperatures that is mainly responsible for restricting lampreys to the cooler river systems of the world. In Western Australia, larval lampreys are currently found in sizable numbers in rivers at a latitude of 34–35°S, very restricted in abundance at 33°S and absent at 32°S and northwards. It is thus probably of significance that lampreys are not found in Africa, where the most southern rivers are located at ~33–34°S. In the context of temperature, the laboratory experiments of Reynolds and Casterlin (1978) have shown that sea lamprey ammocoetes exhibit a preference for temperatures of 10–19°C.

The inability of larvae to survive at temperatures much above 28–30°C may be due, amongst other factors, to the presence of weak bonds in thermolabile enzymes, which tend to dissociate at high temperatures (Hockachka and Somero 1973), or to the melting of cellular and subcellular membrane lipids so that they become freely permeable (Prosser 1973).

SALINITY

The fact that the adults of various parasitic lampreys are adapted to living in environments of different salinities and in freshwater has undoubtedly been of great importance in enabling the larval stages of the Petromyzoniformes to colonize a large number of river systems. Thus, whereas the anadromous parasitic form of the sea lamprey is often found feeding in full strength seawater (~35‰), the landlocked form is adapted to a parasitic existence in a lacustrine environment (Smith 1971; Mathers and Beamish 1974; Beamish et al. 1978; F. W. H. Beamish 1980). While some other parasitic species, such as *Eudontomyzon danfordi*, are found in large fluviatile systems, the Caspian lamprey, *Caspiomyzon wagneri*, spends its adult trophic life in salinities intermediate between those of freshwater and typical marine environments.

BODY SIZE

Although our knowledge of the parasitic phase of anadromous species is relatively limited, it would appear that those lampreys which attain the greatest size travel the farthest distances from the coast. This point is illustrated in the Mediterranean by the contrast between the coastal occurrence of *Lampetra fluviatilis* and the more offshore distribution of *P. marinus* (Zanandrea 1959a; 1962). Like the European river lamprey, the relatively small *Lampetra ayresii* has been found feeding in large numbers in the Straits of Georgia on the west coast of North America (R. J. Beamish 1980). By contrast, *G. australis*, which also characteristically attains a long length, has been obtained in the waters off South Georgia (Permitin 1966; Ivanova-Berg 1968) and in large numbers from the nests of albatrosses on this subantarctic island (Potter et al. 1979). This information indicates that *G. australis* travels very large distances from their natal streams in South America and possibly also the Falkland Islands.

In general, the larger the size attained by a species, the greater the range of its distribution. Thus, the large *P.*

marinus is found in river systems on both sides of the Atlantic, while the smaller *L. fluviatilis* is restricted to European watersheds (Hubbs and Potter 1971). Likewise, the largest of the Southern Hemisphere species, *G. australis*, occurs in South America, Australia, and New Zealand, whereas the two smaller parasitic species of *Mordacia* are restricted, respectively, to southeastern Australia (including Tasmania) and the west coast of South America (Potter and Strahan 1968; Hubbs and Potter 1971). A species that reaches a considerable length but has a restricted distribution is *C. wagneri*, which is represented by a large population in the Caspian Sea. The freshwater parasitic lampreys, such as *E. danfordi*, *Ichthyomyzon unicuspis*, *I. castaneus*, and *I. bdellium*, are also restricted in distribution, the former occurring only in the Danube and the last being present mainly in restricted parts of the Mississippi faunal area (i.e. tributaries to the Gulf of Mexico, Gulf of St. Lawrence and Hudson Bay). In the context of the distribution of the parasitic species of *Eudontomyzon* and *Ichthyomyzon*, it is almost certainly of significance that they are found only in large river systems which support a sufficiently abundant host population.

ANCESTRY

In many cases, the distribution of the nonparasitic species is similar to that of the parasitic species from which it is believed to have been derived (Hubbs 1925; Hardisty and Potter 1971b; Vladykov and Kott 1979a). This generalization thus applies, for example, to pairs of species found in the genera *Ichthyomyzon*, *Tetrapleurodon*, *Mordacia*, and *Lampetra* (Hubbs and Trautman 1937; Álvarez del Villar 1966; Potter 1968; Potter and Osborne 1975). In some situations, however, the nonparasitic lamprey is found far outside the range of any possible ancestor. Examples of such species are provided by the Gulf brook lamprey, *Lampetra meridionalis*, which occurs in the eastern tributaries of the Gulf of Mexico far to the south of the parasitic ancestor from which it is believed to have been evolved (Vladykov and Kott 1979a). Hubbs and Potter (1971) also suggested that *Lampetra zanandreai*, which is only found in the Po Plain in Italy, may also be a southern relict derivative of *Lampetra japonica*. However, on the basis of comments made by Zanandrea to Vladykov regarding the dentition of this species (V. D. Vladykov, University of Ottawa, Ottawa, Ont., personal communication), Vladykov and Kott (1979a) regard *L. zanandreai* as a second nonparasitic derivative of *L. fluviatilis*. On the west coast of North America, the nonparasitic *L. lethophaga* is found only in southern Oregon and northern California, i.e. in the southernmost part of the range of the ancestral *L. tridentata*. Hubbs and Potter (1971) believed that the species they tentatively called *Okkelbergia aepyptera*, but which Vladykov and Kott (1976a, 1979a) place in the genus *Lampetra*, is not only another southern relict, but is also unattached, i.e. there is no lamprey in the contemporary fauna similar to that of its parasitic ancestor. However, this species is regarded by Vladykov and Kott (1979a) as a derivative of *L. ayresii*.

The reader is referred to the species notes for an account of the distribution of the various lampreys and also to the account given by Hubbs and Potter (1971) and Vladykov and Kott (1979b).

Taxonomic Characters Used in Lamprey Systematics

Although the characters used extensively in taxonomic studies for describing lampreys are the product of a number of different investigations (see Hubbs and Potter 1971), particular mention should be made of the contributions of Hubbs and Trautman (1937), Vladykov (1949, 1950, 1955), Vladykov and Follett (1958, 1965, 1967), and Vladykov and Kott (1976b). As a result of these studies, the taxonomic descriptions of ammocoetes now emphasize the patterns of pigmentation on the tail, body surface, peritoneum, and the "tongue" precursor, and the number of trunk myomeres and the proportional measurements for various parts of the body, such as the prebranchial, branchial, trunk, and tail regions. The number of trunk myomeres, the shape and number of the velar tentacles, and also a wide range of body proportions, including those listed above, together with the lengths of the oral disc, the height of the fins, and the diameter of the eye, are also important taxonomic criteria for distinguishing the adults of the various species and genera (Fig. 1). There is little doubt, however, that at this latter stage in the life cycle, the size, number, and arrangement of the lingual and oral disc teeth are of major importance, especially in attempting to establish phyletic relationships among genera.

BODY PROPORTIONS AND MYOMERE COUNTS

Body proportions are useful not only as a taxonomic character, but also as an aid for categorizing stages in metamorphosis and providing important quantitative data on the way in which certain fundamental changes take place during the transition from larva to adult (Manion and Stauffer 1970; Potter et al. 1978, 1980; Bird and Potter 1979a). It is important to recognize that these body proportions often change during sexual maturation, a feature particularly well exhibited by Southern Hemisphere lampreys (Potter and Strahan 1968). Since some of these body intervals have been measured by slightly different means, Fig. 1 illustrates a way in which the method of measurement could be standardized.

Attention is drawn to the ways in which the measurements of body intervals differ in a few small respects from those used by some other workers. Measurements of the four main regions of the body, namely the prebranchial, branchial, trunk, and tail regions, are made sequentially along the longitudinal axis of the body, using the terminal point for one as the initial point for the text. This method has the advantage that the values for these four major body proportions, when expressed as a percentage of the

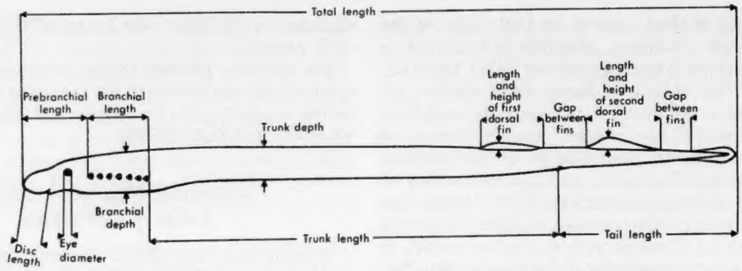

FIG. 1. Diagrammatic representation of a postlarval stage in the life cycle of lampreys showing the various body regions that can be measured for taxonomic and other purposes. Precise descriptions of the method of measurement are given in Bird and Potter (1979b) and Potter et al. (1980).

total length, add up to 100%. The height of the fins are measured vertically, rather than along the highest fin ray as in some other studies. While the latter method is entirely adequate for measurements on adults, it has sometimes proved rather difficult to use in the earliest stages of metamorphosis when the fins are very small. With respect to the trunk region, it is also worth noting that Hubbs and Trautman (1937) have given the following excellent account as to how the number of trunk myomeres should be counted. "The first myomere counted is the one whose posterior septum passes distinctly and entirely behind the groove which surrounds the fringed margin of the last gill opening, so as to leave a definite though often narrow band of muscle between the last groove and the septum. The last myomere counted is the one whose lower posterior angle lies in part or wholly above the cloacal slit."

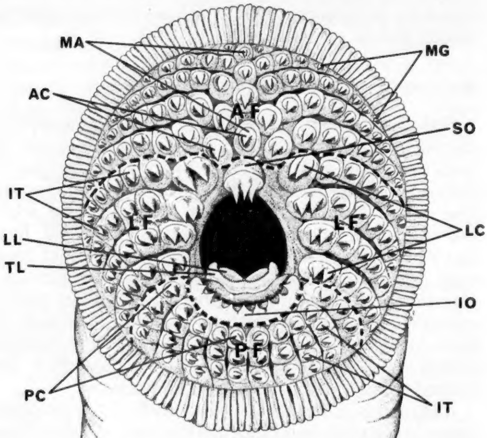

FIG. 2. Dentition of *Ichthyomyzon bdellium*, with a guide to the nomenclature of the laminae, teeth, rows, and fields (see text). In this and the other dentition figures, the oral fimbriae have not been delineated in detail for either form or number (from Hubbs and Potter 1971).

DESCRIPTION AND TERMINOLOGY OF DENTITION

There has been considerable discrepancy in the terminology used for the various tooth series. For this reason, and because of its classificatory and phylogenetic relevance, the following account gives the descriptions provided by Hubbs and Potter (1971) which will also be used in this paper (Fig. 2).

Lingual lamina — The multicuspid teeth of the tongue are borne on a single transverse lingual lamina (TL) and a pair of longitudinal lingual laminae (LL).

Supraoral (SO) — The tooth plate immediately anterior to the front edge of the esophageal opening, behind the anterior circumorals.

Infraoral (OR) — The tooth plate lying immediately distal to the posterior edge of the esophageal opening and the posterior circumorals.

Circumoral row — The circumoral row is defined as comprising those teeth forming a single continuous or subcontinuous series around the esophageal opening, but outside the supraoral and infraoral plates and within the intermediate disc teeth, if developed. They are particularly distinctive as a series in *Ichthyomyzon*, *Petromyzon*, *Caspiomyzon*, and *Geotria* (Fig. 2, 3, 4), but in the anterior part of the disc are not quite as clearly delimited in most other genera, because in the phyletic series the teeth increasingly assume an alternating, quincunx arrangement. The circumoral row may be divided into the anterior (AC), lateral (LC), and posterior circumorals (PC). The lateral circumorals are enlarged and strengthened (only slightly in *Ichthyomyzon*, *Caspiomyzon*, and *Geotria*) and generally begin just anterior to (*Petromyzon*), or opposite, the supraoral; the last one lies close to the outer edge of the infraoral. The anterior and posterior circumorals are those members of the series connecting, respectively, the lateral circumorals anteriorly and posteriorly. In the most

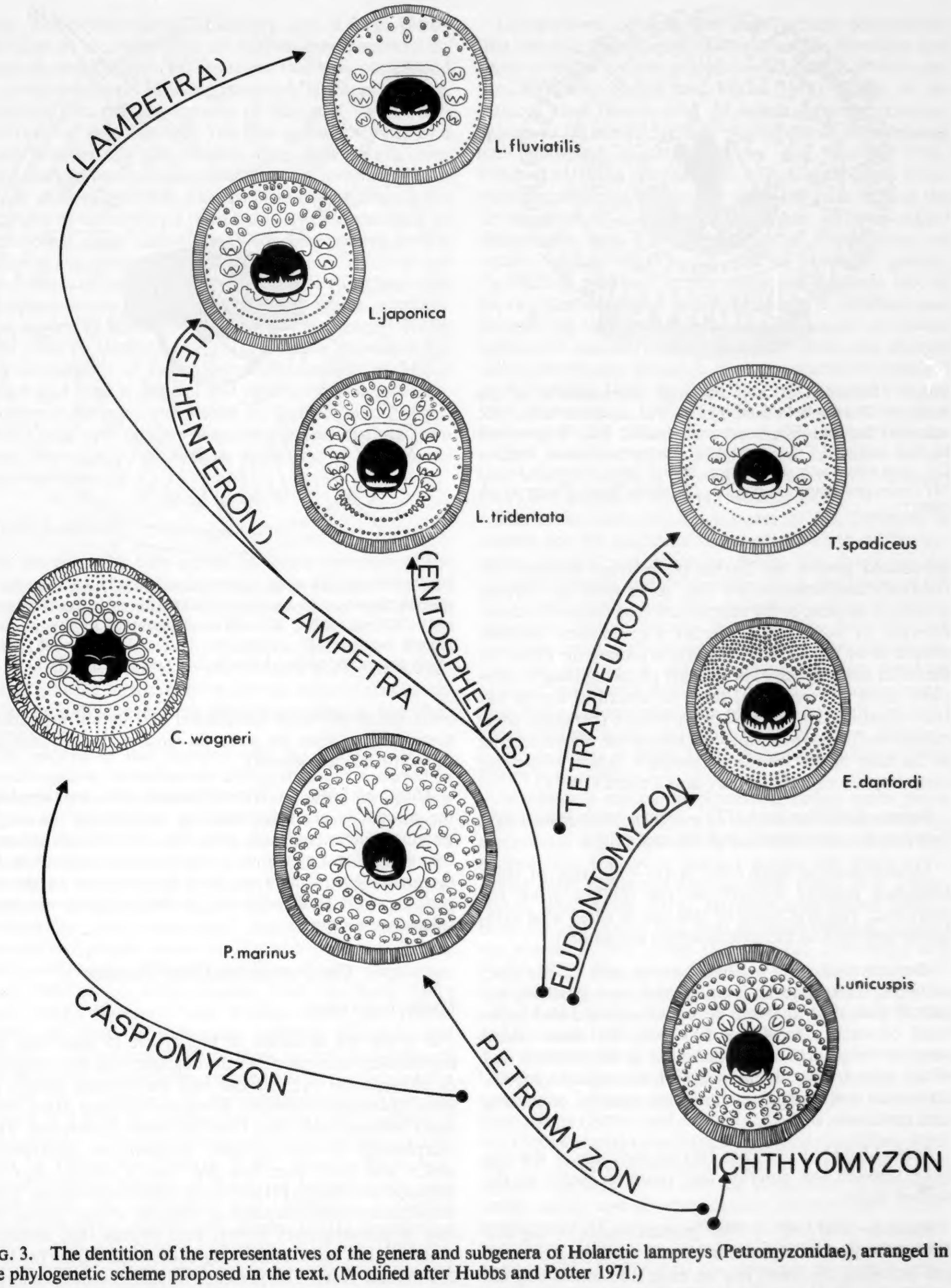
(LAMPETRA)
L. fluviatilis
L. japonica
(LETHENTERON)
L. tridentata
(ENTOSPHENUS)
LAMPETRA
T. spadiceus
TETRAPLEURODON
C. wagneri
E. danfordi
EUDONTOMYZON
P. marinus
I. unicuspis
CASPIOMYZON
PETROMYZON
ICHTHYOMYZON

FIG. 3. The dentition of the representatives of the genera and subgenera of Holarctic lampreys (Petromyzonidae), arranged in the phylogenetic scheme proposed in the text. (Modified after Hubbs and Potter 1971.)

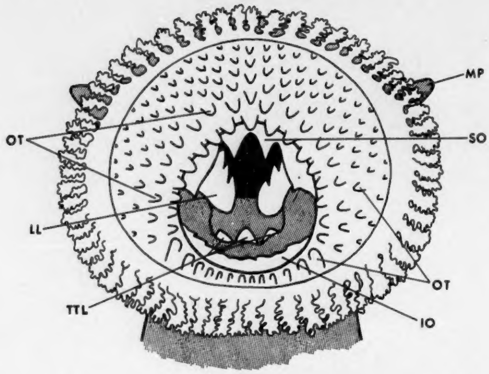

FIG. 4. Dentition of a young adult representative of the Southern Hemisphere lamprey *Geotria australis* Gray. IO, infraoral lamina; SO, supraoral lamina; LL, longitudinal lingual lamina; TTL, tridentate transverse lingual lamina; OT, oral disc teeth of anterior, lateral, and posterior fields; MP, enlarged marginal papilla. (Modified from Potter et al. 1980.)

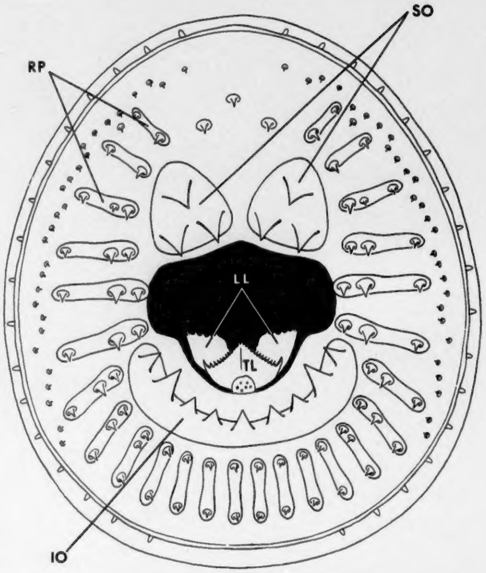

FIG. 5. Dentition of an early spawning-run representative of the Southern Hemisphere lamprey *Mordacia mordax* (Richardson). SO, supraoral; IO, infraoral lamina; LL, longitudinal lingual laminae; TL, transverse lingual lamina; RP, radial tooth plates. (Modified from Hubbs and Potter 1971.)

specialized genera the distinction between anterior circumorals and intermediate disc teeth tends to become arbitrary, because of the alternation. The criterion recommended for inclusion is whether a given tooth extends inward to or beyond the curved line joining the center of the other circumorals. The validity of recognizing a complete series of circumoral teeth as described above has been questioned by Vladykov and Kott (personal communication). However, they do follow the above scheme in the case of the lateral circumorals, which they term inner laterals as in Vladykov and Follett (1967).

Intermediate disc teeth (IT) — Those teeth intervening between the circumorals and the marginals.

Median anterior tooth row (MA) — The row of teeth extending straight forward on the midline from the supraoral. The first tooth of this row is often also arbitrarily definable as the anteromedian circumoral.

Anterior field (AF) — That anterior area of the disc, excluding the supraoral, lying between and including the pair of alate rows that can be traced outward and backward on each side of the disc from the most lateral anterior circumoral to the marginal at the extreme end of the curved rows. All the teeth of this region comprise alate rows emanating from a median–anterior or circumoral row tooth.

Lateral field (LF) — That area on each side of the disc lying between the anterior and posterior fields as described herein.

Posterior field (PF) — That posterior area of the disc behind (and excluding) the infraoral; extending between and including the tooth row on each side connecting the most lateral posterior circumoral and its corresponding marginal (or, when the posterior circumorals are lacking, the comparable position).

Marginals (MG) — Where the alate rows are complete, the marginals are interpreted as comprising the single terminal elements of each alate row, even though one or a few more distal elements in the row may appear to be marginal. Where the alate rows are toothless inside the periphery, all teeth adjacent to the periphery are considered as marginals.

The Petromyzoniform Families

FOSSIL LAMPREYS

It is not the intention of this article to deal with the relationship between either the hagfishes and the lampreys or between the cyclostomes and the various groups of fossil agnathans. However, attention is drawn to the only fossil lamprey that has thus far been discovered. The morphology of this animal, *Mayomyzon pieckoensis*, which was only described just over a decade ago by Bardack and Zangerl (1968) from material collected from mid-Pennsylvanian deposits in Illinois, is very similar to that of contemporary forms. This implies that lamprey evolution has been remarkably conservative over the last 280 million years. The presence of such features as large eyes, well-developed gill chambers, and a large piston cartilage in the specimens of *Mayomyzon* examined by Bardack and Zangerl (1971) suggest that they correspond to postlarval stages of living lampreys. If this is the case, there are two striking features of relevance to an interpretation of their biology. The first is that they are of a much smaller size (30–60 mm) than that of any contemporary lamprey at the completion of metamorphosis, which almost certainly has implications regarding the duration of larval life, if indeed this species possessed an ammocoete stage (Hardisty 1979). The second feature concerns the relatively small size of the buccal funnel and the absence of teeth on the oral disc, which suggests that *Mayomyzon* was less predaceous than extant lampreys. The reader is referred to Bardack and Zangerl (1968, 1971) and to Hardisty (1979) for a much more comprehensive account of the characteristic features of *Mayomyzon* and their biological and phylogenetic significance. This fossil lamprey was placed by Bardack and Zangerl (1971) in a new family, Mayomyzonidae, distinct from those containing the extant members of the Petromyzoniformes.

LIVING LAMPREYS

It has generally been agreed by major reviewers of the taxonomy of Holarctic lampreys that all the Northern Hemisphere genera should be placed in a single family (Regan 1911; Creaser and Hubbs 1922; Holly 1933; Berg 1948; Fontaine 1958; Vladykov and Follett 1967). In this context, Valdykov and Gruchy (1975) have suggested that the correct spelling for the name of this family is Petromyzonidae and not Petromyzontidae as has often been used.

In contrast to the situation with the Northern Hemisphere species, considerable disagreement has existed in the past over the taxonomic relationship of the two Southern Hemisphere genera *Geotria* and *Mordacia*. Some authors for example have separated *Mordacia* from *Geotria* and the Holarctic genera at either the subfamily (Rauther 1924; Holly 1933; Berg 1940; Fontaine 1958) or family levels (Gill 1893; Ogilby 1896; Waite 1921). Other taxonomists have considered that the two Southern Hemisphere genera should be placed together in either a single subfamily (Nikolskii 1954) or family (Eigenman 1928; McCulloch 1929; Fowler 1940; de Buen 1961; Scott 1962). However, both Whitley (1932) and Hubbs (1947) felt that the differences between *Mordacia* and *Geotria*, and between both of these genera and those of the Northern Hemisphere, merited a tripartite separation of the living lampreys at the familial level. While the results of a later detailed morphological and anatomical examination were used in support of a tripartite subdivision by Potter and Strahan (1968), these workers suggested that the division of the living lampreys was best achieved at the subfamily level. However, a further investigation by Hubbs and Potter (1971), employing some additional criteria, suggests that the Holarctic genera and *Mordacia* and *Geotria* are sufficiently distinct to merit separate family status.

Comparisons between the three groups demonstrate that *Geotria* shares some characters with *Mordacia* and some with the various petromyzonid genera (Potter and Strahan 1968; Hubbs and Potter 1971). Some of the features that *Geotria* and *Mordacia* have in common appear to be related to their possession of an extremely long spawning migration (Potter and Strahan 1968; Potter et al. 1968a; Potter 1970; unpublished data). Thus, the changes during this period of the life cycle include the development of a much more extreme form of sexual dimorphism and a greater degree of modification of certain features than is the case in Holarctic genera. Particularly pertinent in this respect is the large size of the oral disc developed by all mature male *Mordacia* and *Geotria*, the very well-developed gular pouch of mature males of *G. australis* and *M. lapicida*, and the vast changes undergone by the dentition during maturation (Maskell 1929; Strahan 1959; de Buen 1961; Potter and Strahan 1968; Potter et al. 1968a; Hubbs and Potter 1971; Hardisty and Potter 1971a). Another feature of both groups is their possession of a well-developed midgut diverticulum, which is single in *Mordacia* (Strahan and MacLean 1969) and double in *Geotria* (Maskell 1930).

The main distinguishing features of the dentition of *Geotria* are the spatulate shape of the teeth of the anterior, lateral, and posterior fields, the shape of the supraoral lamina and its location under the apices of the circumoral series, and the possession of a tridentate transverse lingual lamina (Fig. 4). The last of these structures becomes bidentate during the upstream migration. In *Geotria*, a unique separation also develops between the second dorsal and caudal fins during metamorphosis and the coloration of the macrophthalmia and adult feeding stages is unlike that of other lampreys (Strahan 1959; de Buen 1961; Potter and Strahan 1968; Potter et al. 1980).

Mordacia is unique in possessing radial tooth plates (Fig. 5), which break down as the animal nears maturity, a supraoral region containing two tricuspid elements and a distinctive transverse lingual lamina (de Buen 1961; Potter 1968; Potter and Strahan 1968; Potter et al. 1968a; Hubbs and Potter 1971; Hardisty and Potter 1971b). Both the parapineal and oral fimbriae (fringed lappets) are absent in this genus (Eddy 1972; Lethbridge and Potter 1979). The eyes are located dorsolaterally, rather than laterally as in other genera, a feature which is probably related to the burrowing habits of the adult (Potter and Strahan 1968; Potter et al. 1968a).

A comparison of the hemoglobin electrophoretic patterns of *Mordacia* and *Geotria* has shown no close correspondence between the bands in either their larvae or their adults (Potter and Nicol 1968). It is also clear that the chromosomal constitution of *Mordacia* differs from that of Holarctic lampreys and also *Geotria*. Thus, diploid numbers of 76 and the possession of predominantly meta- and submeta-centric chromosomes in *M. mordax* and *M. praecox* (Potter et al. 1968b; Robinson and Potter 1969) may be contrasted with chromosome numbers of 164–168 and the presence of mainly acrocentric chromosomes in several different Holarctic species (see Robinson et al. 1974). Preliminary work on *G. australis* suggests that the diploid number of this species is higher than those of Northern Hemisphere lampreys.

On the basis of the comparisons made between the various genera of lampreys, Hubbs and Potter (1971) considered that the Petromyzoniformes were appropriately divided into the Petromyzonidae, Geotriidae, and Mordaciidae. This view is still retained by the author of this paper.

PHYLOGENY BASED PRIMARILY ON DENTITION

Evidence that the Petromyzonidae are a relatively compact group is provided by the fact that, on the basis of their dentition, the species can be arranged in a logical and interconnected series (Fig. 3). Key characters for the different genera have been presented by Vladykov and Follett (1967), Hubbs and Potter (1971), and Vladykov and Kott (1979b). Although opinions differ between workers as to whether *Entosphenus*, *Lethenteron*, and *Lampetra* should be regarded as subgenera or genera, and whether or not *aepyptera* should be placed in the genus *Lampetra* (Vladykov and Follett 1967; Hubbs and Potter 1971; Vladykov and Kott 1976a, 1979c), the main characters for most of the taxonomic groups are in broad agreement.

The most simple dentitional arrangement, and almost certainly the most primitive, is found in *Ichthyomyzon* (Hubbs and Trautman 1937). Thus, in *I. unicuspis*, which is regarded as the ancestral stock within this genus, the very simple isomerous teeth are arranged in a series of alate rows showing little or no differentiation (Fig. 3). The trend in this genus is for an increasing modification of the circumoral series with the result that in *I. bdellium*, the most advanced of the three parasitic species, all the lateral circumorals are bicuspid. The presence of alate rows extending throughout the whole of the anterior, lateral, and posterior fields is also found in the proposed derivative genera, *Petromyzon* and *Caspiomyzon*, but in the case of spawning-run *Caspiomyzon* the teeth have become modified to form rounded tubercles. A characteristic of *Ichthyomyzon*, *Petromyzon*, and *Caspiomyzon* is the possession of a supraoral tooth, which is not markedly different from those of the circumoral series.

All other genera, and subgenera of Holarctic lampreys differ from *Ichthyomyzon*, *Petromyzon*, and *Caspiomyzon* in having a wide supraoral lamina rather than a single or multicuspid supraoral tooth (Fig. 3). The teeth of their lateral and posterior fields also differ in no longer having a series of complete alate rows. On the basis of dentition, these Holarctic lampreys appear to have followed one of two main lines from stocks possessing characters similar to those of *Petromyzon*. The main trend in the *Eudontomyzon* and *Tetrapleurodon* lineages has been for a great increase in both the numbers of teeth and tooth rows. During this process, the teeth have declined in size and become more villiform. However, it should be noted that the trend towards a loss of a complete series of alate rows in the posterior field has progressed further in *Tetrapleurodon* than in *Eudontomyzon*. The increase in the number of teeth in this lineage is well illustrated by the presence of 8–12 anterior circumoral teeth in *E. danfordi* (Zanandrea 1959a), which is much greater than is the case in *Ichthyomyzon*, *Petromyzon*, and *Caspiomyzon*.

The numbers of teeth given above for the anterior circumoral series is about twice that found in *Entosphenus*, which is considered as the base for the second main lineage arising from a *Petromyzon*-like lamprey (Fig. 3). The main trends seen in this proposed lineage are the enlargement of the lateral circumorals, paralleling the development of a wide supraoral lamina, and a progressive loss of teeth in all three fields. In *Entosphenus*, the remnants of the intermediate teeth are present just inside the marginals in the lateral field, and the more lateral of the posterior circumorals tend to be bicuspid. These features are retained by *Lethenteron*, with the exception that the posterior circumorals are smaller and uniformly unicuspid, and the number of lateral circumorals is reduced on each side from four to three. In *Lampetra*, the terminal taxon in this proposed lineage, the posterior circumoral row teeth are no longer present.

In discussions as to whether *Entosphenus*, *Lethenteron*, and *Lampetra* should be regarded as genera or subgenera, the question of intergradation of characters between the members of the various groups is of importance. The tridentate supraoral, for example, is not present in all representatives of each *Entosphenus* species and it does occasionally occur in other members of the *Lampetra* subgenera (Hubbs 1971; personal communication). It is also worth noting that posterior circumorals are present only in some representatives of *Lampetra* (*Lethenteron*) *reissneri*, and *Lampetra* (*Lethenteron*) *zanandreai* (see Berg 1931; Zanandrea 1958). Moreover, it is clear that the tooth formula for the lateral circumorals is not consistently 2–2–2 in *Lethenteron* and 2–3–2 in *Lampetra*. With respect to the relationship between *Lethenteron* and *Lampetra*, it is relevant that the amino acid composition of the hemoglobins of *L. japonica* and *L. fluviatilis* are very similar but differ from that found in *P. marinus* (Dohi et al. 1973).

The very considerable differences between the dentition of the Southern Hemisphere lampreys and those of Holarctic genera make it difficult to assess the interrelationships between the groups. However, the dentition of both *Geotria* and *Mordacia* are similar to those of Northern Hemisphere genera in that the teeth of the oral disc also pass out from the oral aperture in the form of alate rows (Fig. 4 and 5). A superficial resemblance can also be seen between the blunt cusps of the teeth of *Caspiomyzon* (Fig. 3) and *Geotria* (Fig. 4). In *Mordacia*, however, the most prominent of the oral disc teeth are uniquely located on elongated plates which extend outwards towards the periphery of the disc from where a number of small discrete teeth then curve sharply downwards. During the course of the spawning run, the radial plates break down to leave an inner series of teeth in the position which in Holarctic species are occupied by the circumorals (Potter 1968; Potter and Strahan 1968; Potter et al. 1968a; Hardisty and Potter 1971b).

Fundamental differences are also found between the components of the dentition of *Geotria*, *Mordacia*, and the Northern Hemisphere lampreys. For example, the supraoral consists of two tricuspid plates in *Mordacia* (Fig. 5), whereas that of *Geotria* comprises a large spatulate prong at each lateral edge, between which two smaller central, elongated and pointed cusps are present (Fig. 4). By contrast, the supraoral of Holarctic genera varies from a small central cusp in primitive groups to a wide lamina in the more advanced taxa. The structure of the transverse lingual lamina also differs between the three groups. The most divergent form is found in *Geotria* where the strongly trident structure is gradually changed to a bident arrangement during the spawning run (Maskell 1929). This contrasts with the straight or triangular structure present in both *Mordacia* and the petromyzonids. Even in this character, however, *Mordacia* differs from Holarctic species in having the lateralmost cusps, rather than the median, if any, enlarged.

While interrelationships between the Northern and Southern Hemisphere lampreys must be postulated with caution, the presence of a basic alate arrangement to the teeth of the oral disc is a particularly striking common character. In this context, the relatively simple pattern and the presence of simple pointed teeth found in such Holarctic genera as *Ichthyomyzon* and *Petromyzon*, suggests that these two genera are closer to an ancestral lamprey stock than *Mordacia* and *Geotria*, in which the tooth arrangements are apparently more specialized.

List of Lamprey Genera and Species

The following account is based on the species lists given by Hubbs and Potter (1971) and Vladykov and Kott (1979b).

Genus *Ichthyomyzon* Girard, 1858

A taxonomically compact group confined to freshwaters of North America. The six species can be grouped into three pairs, each containing an ancestral parasitic species and a nonparasitic derivative.

Ichthyomyzon unicuspis Hubbs and Trautman, 1937.

The silver lamprey is a parasitic species which occurs in the Hudson Bay, Great Lakes, and St. Lawrence River systems and in the Mississippi River drainage from South Dakota to Pennsylvania and New York.

Ichthyomyzon fossor Reighard and Cummins, 1916.

The northern book lamprey is the nonparasitic derivative of *I. unicuspis* and is found from Manitoba and eastern Wisconsin across Michigan to northern Indiana and Ohio to the Ohio River drainage; also in southcentral Missouri.

Ichthyomyzon castaneus Girard, 1858.

The chestnut lamprey is a parasitic species probably derived from *I. unicuspis*. It occupies the northwesterly and far southern parts of the Mississippi River system and other Gulf of Mexico rivers; also in lakes Michigan, Manitoba, and Winnipeg.

Ichthyomyzon gagei Hubbs and Trautman, 1937.

The southern brook lamprey occurs throughout the southern part of the range of its presumed ancestral species, *I. castaneus*, ranging from southern Missouri to eastern Texas and western Florida.

Ichthyomyzon bdellium (Jordan, 1885).

The Ohio lamprey is a parasitic species that is believed to have been derived from *I. castaneus*. It is found throughout the Ohio River system, including the Wabash and Upper Tennessee rivers.

Ichthyomyzon greeleyi Hubbs and Trautman, 1937.

The allegheny or mountain brook lamprey is a nonparasitic derivative of *I. bdellium* found in mountain tributaries of the Ohio River system in New York, Ohio, West Virginia, and Kentucky. *Ichthyomyzon hubbsi*, a second nonparasitic derivative of *I. bdellium*, was described by Raney (1952) from material collected in the upper Tennessee River system. However, Vladykov and Kott (1979b) consider this species to be indistinguishable from *I. greeleyi*.

Genus *Petromyzon Linnaeus*, 1758

This is the only petromyzonid genus, other than *Caspiomyzon*, which does not contain a nonparasitic species.

Petromyzon marinus Linnaeus, 1758.

The sea lamprey is represented by anadromous popuations in the Atlantic drainages of North America to as far south as Florida and the Gulf of Mexico, and in Europe from Iceland and the Barents Sea to as far southeast as the western part of the Mediterranean. Landlocked derivative stocks are found in lakes Cayuga, Seneca, Oneida, Champlain, and also each of the Great Lakes.

Genus *Caspiomyzon* Berg, 1906

This genus is characterized by the rounded nature of the teeth and by the absence of any nonparasitic species.

Caspiomyzon wagneri (Kessler, 1870).

The Caspian lamprey is an anadromous species restricted to the Caspian Sea and its tributaries. The structure of its teeth suggests that during the adult trophic phase it may feed in a manner different to that of typical parasitic species (see Hubbs and Potter 1971).

Genus *Eudontomyzon* Regan, 1911

Although *Eudontomyzon* was regarded by Berg (1931) as a subgenus of *Lampetra*, Hubbs and Potter (1971) preferred to retain its generic status on the basis of its dentitional characters and its position on an apparently distinct phyletic line. *Eudontomyzon* is confined to fresh water and contains both parasitic and nonparasitic species.

Eudontomyzon danfordi Regan, 1911.

The Hungarian lamprey is a parasitic species found in the Danube Basin.

Eudontomyzon vladykovi Zanandrea, 1959.

Eudontomyzon vladykovi, a nonparasitic derivative of *E. danfordi*, is present only in the drainage system of the Danube River.

Eudontomyzon mariae Berg, 1931.

The Ukrainian lamprey is a nonparasitic species which, like *E. vladykovi*, is also probably derived from *E. danfordi*.

Eudontomyzon gracilis Kux, 1965.

The Slovakian lamprey is a nonparasitic species with a restricted distribution in Slovakia.

Eudontomyzon morii Berg, 1931.

The Korean (or Manchurian) lamprey, which is found in effluents of the Yellow Sea, is apparently a parasitic species. It may be regarded as an example of a far southern relict.

Genus *Tetrapleurodon* Creaser and Hubbs, 1922

Tetrapleurodon is another example of a far southern relict lamprey, being found only in the highly distinctive fauna of the Río Lerma system at the southern end of the Mexican plateau.

Tetrapleurodon spadiceus (Bean, 1887).

The parasitic Mexican lamprey is a freshwater species found in the Río Lerma system.

Tetrapleurodon geminis Álvarez del Villar, 1966.

The nonparasitic Mexican lamprey is found in the same drainage basin as *T. spadiceus*, the species from which it is believed to have been derived.

Genus *Lampetra* Gray, 1851

The genus *Lampetra* was used by Hubbs and Potter (1971) to include three subgenera; namely *Entosphenus*, *Lethenteron*, and *Lampetra*. This grouping was based on the similarity in the general plan of their dentition, and in the overlap found in some characters, particularly amongst nonparasitic species. In contrast to this broader application of the term *Lampetra*, Vladykov and Follett (1967) and Vladykov and Kott (1976a, b, 1979b) have expressed a strong preference for *Entosphenus*, *Lethenteron*, and *Lampetra* as distinct genera.

Subgenus *Entosphenus* Gill, 1862

Lampetra (Entosphenus) tridentata (Richardson, 1836).

The Pacific lamprey is an anadromous species which spawns in rivers of the Pacific Ocean basin from Alaska to California. Like the sea lamprey, the Pacific lamprey has apparently given rise to landlocked parasitic forms.

Lampetra (Entosphenus) minima Bond and Kan, 1973.

This dwarfed parasitic lamprey from Miller Lake, Oregon, is apparently now extinct.

Lampetra (Entosphenus) similis (Vladykov and Kott, 1979).

This parasitic lamprey has been collected in the Klamath River in California and Oregon.

Lampetra (Entosphenus) lethophaga Hubbs, 1971.

This nonparasitic derivative of *L. tridentata* is found in the basin of the Pit River, a main upper tributary of the Sacramento River in California, and from the adjacent Klamath River system in Oregon.

Lampetra (Entosphenus) folletti (Vladykov and Kott, 1976).

This nonparasitic lamprey is found in the Klamath River system in California.

Lampetra (Entosphenus) hubbsi (Vladykov and Kott, 1976).

This nonparasitic lamprey, which now has a very limited distribution in California, probably originated in the Kern River.

Subgenus *Lethenteron* Creaser and Hubbs, 1922

Lampetra (Lethenteron) japonica Martens, 1868.

The Arctic lamprey is an anadromous parasitic species which is found eastwards from the region of Varangar Fjord through Siberia and eastward along the eastern Pacific coast to Japan, and also occurs in Alaska and northern Canada. It has been suggested that the landlocked form of the Arctic lamprey, *L. japonica kessleri*, is a distinct species from the anadromous form *L. japonica septentrionalis* (Poltorhykhina 1974).

Lampetra (Lethenteron) lamottenii (Lesueur, 1827).

The American brook lamprey is found only in the more eastern and southern regions of North America, being present in the tributaries of the Great Lakes, the St. Lawrence and Mississippi river systems, and in rivers tributary to the Atlantic between New Hampshire and North Carolina. Although its current distribution differs from *L. japonica*, it is almost certainly a derivative of this parasitic species.

Lampetra (Lethenteron) reissneri (Dybowski, 1869).

The Pacific brook lamprey, like the American brook lamprey, is believed to be a nonparasitic derivative of *L. japonica*. It occurs in Japan and on the eastern coast of Asia from Vladivostok northward to the rivers entering the Sea of Okhotsk.

On the basis of its myomere number (56–59), Vladykov and Kott (1978a) have suggested that *Lampetra mitsukurii* Hatta, 1911, another Japanese nonparasitic derivative of *L. japonica*, is synonymous with *L. reissneri* for which they give a range in myomere number of 57–63.

Lampetra (Lethenteron) meridionalis (Vladykov, Kott, and Pharand-Coad 1975).

The Gulf brook lamprey, which is a third nonparasitic derivative of *L. japonica*, has a very restricted distribution which partly overlaps the southern end of the range of *L. lamottenii* (Vladykov and Kott 1978a). It has been found in tributaries of the Tennessee River of the Mississippi system in Tennessee, and the Tombigbee and Alabama rivers in Alabama and Georgia (Vladykov et al. 1975).

Lampetra (Lethenteron) alaskensis (Vladykov and Kott, 1978).

The Alaskan lamprey is a nonparasitic species limited to northwestern North America where it is sympatric with the ancestral *L. japonica*.

Lampetra (Lethenteron) matsubarai (Vladykov and Kott, 1978).

This fifth nonparasitic species derived from *L. japonica* occurs in Hokkaido, Japan, and the Kamchatka Peninsula. This corresponds to the *mitsukurii* group with high myomere numbers listed in Hubbs and Potter (1971).

Lampetra (Lethenteron) zanandreai Vladykov, 1955.

This brook lamprey is found in the Po Plain in northern Italy. There is some disagreement as to whether this species should be placed in what are referred to in this paper as the subgenera *Lampetra* or *Lethenteron*. On the basis of the cusp formula of the lateral circumorals and the presence of posterior circumorals recorded by Zanandrea (1959b), Hubbs and Potter (1971) considered that it should be placed in *Lethenteron*. In view of the very low number of trunk myomeres it possesses, Hubbs and Potter (1971) also suggest that it could be an ancient southern relict of *Lampetra* (*Lethenteron*) *japonica*. This view is not supported by Vladykov (University of Ottawa, personal communication), who states that Zanandrea had admitted to making a mistake regarding the posterior circumorals. For this reason, Vladykov and Kott (1979b) regard *zanandreai* as having much more affinity with *Lampetra* (*Lampetra*) *fluviatilis* and *Lampetra* (*Lampetra*) *planeri*.

Subgenus *Lampetra*

Lampetra (Lampetra) fluviatilis (Linnaeus, 1758).

The European river lamprey spawns in western European watersheds of the Atlantic, Baltic, and Mediterranean. The spawning-run populations consist of "typical" and "praecox" forms which differ in size (Berg 1948; Abou-Seedo and Potter 1979). Landlocked populations are present in Lake Ladoga in the Baltic.

Lampetra (Lampetra) planeri (Bloch, 1784).

The European brook lamprey has a very similar distribution to that of the ancestral *L. fluviatilis*.

Lampetra (Lampetra) lanceolata Kux and Steiner, 1972.

The Turkish brook lamprey is found in the Iyidere River in Turkey.

Lampetra (Lampetra) ayresii (Günther, 1870).

Vladykov and Follett (1958) showed that the North American river lamprey was distinct from *L. fluviatilis*, its European analogue. This anadromous parasitic species has been found southwards from the Skeena River in British Columbia to San Francisco Bay, California.

Lampetra (Lampetra) richardsoni Vladykov and Follett, 1965.

The western brook lamprey, which is a nonparasitic derivative of *L. ayresii*, is found in Pacific drainage systems of North America in British Columbia, Washington, and Oregon.

Lampetra (Lampetra) pacifica Vladykov, 1973.

The western Pacific brook lamprey, which is apparently a second nonparasitic derivative of *L. ayresii*, occurs in streams in Oregon and California.

Lampetra (Lampetra) aepyptera (Abbott, 1860).

During the last few years, disagreement has existed as to the systematic position of the nonparasitic lamprey whose specific name is *aepyptera*. On the basis that intramarginal teeth were present in the lateral and posterior fields, Hubbs and Potter (1971) suggested that its origin was from a parasitic lamprey of the *Eudontomyzon/Tetrapleurodon* type, in which these teeth are prominent. However, Vladykov and Kott (1976a) have pointed out that recent studies (e.g. Vladykov et al. 1975) have shown that small numbers of these teeth are also occasionally found in some nonparasitic species of *Lethenteron* and *Lampetra*. For this reason, Vladykov and Kott (1976a) rejected the suggestion made by Hubbs and Potter that "a provisional and noncommittal course" would be to call this species *Okkelbergia aepyptera*, and strongly argued that it should be placed in *Lampetra*. The problem of elucidating the systematic position of *aepyptera* is compounded by the very degenerate dentition found in the representatives of some populations, which, together with its extremely low myomere number (53), suggest that it is a nonparasitic lamprey of considerable antiquity Moreover, the problem is further complicated by the fact that *aepyptera* occurs in the southeastern part of the United States, far from any likely parasitic ancestor. Indeed, *L. ayresii*, the only parasitic representative of the subgenus *Lampetra* found in North America occurs on the west coast of this continent. Thus, while the brook lamprey is tentatively listed in this account as *Lampetra* (*Lampetra*) *aepyptera*, attention is drawn to the problems posed by the degenerate nature of the dentition and the pattern of geographical distribution in elucidating the precise phylogenetic interrelationships of this species. If future work confirms that *aepyptera* is best placed in the genus *Lampetra*, it is conceivable that it is an ancient derivative of *Lampetra* (*Lethenteron*) *japonica*. In this context, it is worth noting that Zanandrea (1958) has drawn a parallel between *zanandreai* and *aepyptera*.

Genus *Geotria* Gray, 1853

Several genera have been synonymized with *Geotria* (Potter and Strahan 1968). The taxonomic confusion that existed in the past can be attributed to the vast changes undergone during the life cycle of the individuals representing what is now regarded as a monotypic genus.

Geotria australis Gray, 1851.

The pouched, wide-mouthed, or long-headed lamprey is an anadromous species which enters the rivers of Tasmania, the southern part of mainland Australia, New Zealand, Chile, and Argentina. It has been collected far from its natal streams in South Georgia in the South Atlantic (Potter et al. 1979). The mature males of *G. australis* possess an extremely large "mouth" and well-developed gular pouch.

Genus *Mordacia* Gray, 1851

Mordacia, like *Geotria*, undergoes very much greater changes during its life cycle than Holarctic lampreys and this has also led to a proliferation of names (Potter and Strahan 1968). At the present time, this genus is recognized as containing two anadromous parasitic and one nonparasitic species.

Mordacia mordax (Richardson, 1846).

The short-headed lamprey is an anadromous parasitic species which enters the rivers of both the southeastern part of mainland Australia and of Tasmania.

Mordacia praecox Potter, 1968.

This nonparasitic derivative of *M. mordax* has thus far only been found in two rivers in New South Wales, Australia.

Mordacia lapicida (Gray, 1851).

This anadromous parasitic species can be regarded as the South American analogue of *M. mordax*. However, unlike *M. mordax* but like *G. australis*, the mature males develop a pronounced gular sac.

Paired Species

INTRODUCTION

The close relationships between the morphology of certain nonparasitic and parasitic lampreys was recognized by Hubbs as long ago as 1925. On the basis of his observations, Hubbs suggested several cases in which a particular nonparasitic species had apparently evolved from a form similar to that of an extant parasitic lamprey. These closely related species with divergent postlarval modes of life were later termed "paired forms" or "paired species" by Zanandrea (1959b). Recent work by Vladykov and Kott (1976a, b; 1979a, b), has shown that some parasitic lampreys have given rise to two or more different nonparasitic derivatives. These workers have therefore suggested that the term "satellite species" would be more appropriate than "paired species" (Vladykov and Kott 1979a). However, in this review the commonly used term "paired species" is retained since it is considered to reflect accurately the relationship between closely related species with different types of life cycle. The following account will focus on a number of documented examples of the way in which changes have taken place in the origin of a nonparasitic lamprey from a particular parasitic species.

Nonparasitic lampreys have been found in all Northern and Southern Hemisphere genera, apart from *Petromyzon*, *Caspiomyzon*, and *Geotria*. While it is possible to "pair" most nonparasitic lampreys with a particular parasitic species, this apparently cannot clearly be done in the case of *Lampetra aepyptera*.

The anatomical studies of Weissenberg (1925, 1926, 1927) on the anadromous parasitic *Lampetra fluviatilis* and its nonparasitic derivative *Lampetra planeri* provided important general information on the pattern of gonadal and gut changes in parasitic and nonparasitic species. These studies, together with more recent investigations (see Hardisty and Potter 1971b), have demonstrated the following important features of nonparasitic lampreys, some of which will be discussed in greater detail later in this paper.

1) Feeding does not occur during postlarval life, when at most the adult foregut is patent for only a short period of time and the intestine starts degenerating a few weeks after the beginning of metamorphosis.
2) The gonads start to mature rapidly ~2 mo after the initiation of metamorphosis, with the result that sexual maturity is reached ~6–10 mo after the completion of larval life.
3) The number of eggs in the mature female is greatly reduced, compared with that found in parasitic species. This feature is a result of massive oocyte atresia during postlarval life.
4) The adults are similar in length to those of their

larger larvae, whereas adults of parasitic species are generally much larger than the greatest size reached by their ammocoetes.

5) Compared with parasitic species, the duration of larval life in nonparasitic species is extended whilst that of the adult phase is reduced.

Morphology of Paired Species

The sexually mature adults of closely related parasitic and nonparasitic lampreys can almost invariably be separated on the basis of body size. However, the same is generally not true of the larval stages where considerable overlap is found in such characters as body proportions and trunk myomere number, and marked similarities are present in the patterns of pigmentation. Indeed, there are few reports of either qualitative, morphometric, or meristic characters being used successfully to distinguish between the larvae of paired species.

One exception to the above generalization regarding ammocoetes was provided by MacDonald (1959), who claimed that in samples from British rivers he could distinguish between the larval stages of *L. fluviatilis* and *L. planeri* on the basis of pigmentation, the relative length of the caudal fin, and the number of trunk myomeres. However, several aspects of these results have posed considerable doubt about the validity of MacDonald's key for distinguishing not only between the larvae of both species of *Lampetra* but also in distinguishing them from *Petromyzon marinus*. For example, MacDonald (1959) gave a mean (67.2) and range (61–69) for the number of trunk myomeres in *P. marinus* which were clearly much lower than those recorded by other workers for this species, both in European and North American rivers (Zanandrea 1957; Vladykov 1949, 1950; Wigley 1959). A similar problem resided in the case of MacDonald's values for the number of trunk myomeres in *Lampetra*. Thus, his counts for *L. planeri* were near the upper end of the range given for this species by other workers, whereas those for *L. fluviatilis* were much lower and showed virtually no overlap with the minimum counts recorded for the river lamprey elsewhere in Europe (for references see Potter and Osborne 1975). The apparent anomalies in MacDonald's key are of importance since the diagnostic characters he gave have subsequently been reproduced in Russian by Ivanova Berg (1962) and in keys to British fishes by Maitland (1972) and Bagenall (1973). Moreover, a recent detailed examination of a variety of taxonomic criteria in the two *Lampetra* species and *Petromyzon* has confirmed the view that MacDonald's results are erroneous (Potter and Osborne 1975). Prior to Potter and Osborne's study, it had been established that the description of the pattern of tail pigmentation in North American and European *Petromyzon* given by Vladykov (1950, 1960), and also by MacDonald (1959), could be used to recognize the larvae of this species in British rivers. The samples of *L. planeri* obtained by Potter and Osborne (1975) came from small rivers, in which extensive sampling for adults had shown they contained only this species. The representatives of *L. fluviatilis* were taken from sites on other rivers which, on the basis of length–frequency data and the capture in several years of large numbers of metamorphosing river lampreys, were believed to contain few, or no representatives of *L. planeri* (Hardisty and Huggins 1970; Potter and Osborne 1975).

The values obtained by Potter and Osborne (1975) for the number of trunk myomeres in ammocoetes of *L. fluviatilis* and *L. planeri* showed a close correspondence with those recorded both by themselves and most other workers for the clearly identifiable upstream migrants or mature adults of these species. The study of *Lampetra* larvae revealed no qualitative or quantitative morphological characters that could be used with certainty to distinguish between the ammocoetes of brook and river lampreys. At the same time, however, differences were found between the mean number of trunk myomeres in the two species. Thus, the value of 61.2 for pooled data from four populations of *L. planeri* differed significantly ($P < 0.001$) from the mean of 62.4 recorded for two populations of *L. fluviatilis*. Moreover, the incidence of pigmentation on the tongue precursor ranged from 74.2 to 83.7% in populations of *L. fluviatilis* compared with 5.1 to 35.6% in *L. planeri*. Although the proportional lengths of the various regions of the body were similar in larvae of comparable size, there were indications that the pattern of change in both tail and trunk length differed slightly (Potter and Osborne 1975). The fact that the various body proportions undergo changes during larval life, particularly in the early stages, emphasizes the importance of making comparisons between values obtained for animals of similar length. Contrary to the findings of MacDonald (1959), no difference could be detected between either the relative length or the pigmentation of the caudal fin of larval *L. fluviatilis* and *L. planeri*. Despite the marked similarity in many ammocoete characters, the study of Potter and Osborne (1975) has demonstrated that significant differences have been developed in the morphology of larvae during the evolution of the nonparasitic brook lamprey from the anadromous parasitic river lamprey.

Certain trends exhibited in the evolution of *L. planeri* from *L. fluviatilis* are also found in other paired species. For example, in the larval stages, a value of 66.8 for the mean number of trunk myomeres in the parasitic *L. ayresii* is greater than the 60.7 and 54.0 recorded for the nonparasitic *L. richardsoni* and *L. pacifica*, respectively (Valdykov and Follett 1958; Vladykov and Kott 1979c). Likewise, anadromous parasitic *L. tridentata* has a greater number of trunk myomeres (67.8) than the 66.3 and 61.8 found in the comparable nonparasitic species *L. lethophaga* and *L. folletti* (Vladykov and Kott 1979a). In representatives of the parasitic *L. japonica* and the nonparasitic *L. matsubarai* taken from the same river, the number of trunk myomeres were 70.5 and 68.5, respectively (Vladykov and Kott 1978b). An even greater difference between the number of trunk myomeres in the parasitic and nonparasitic species is found in the cases of *L. japonica* (69.5) and *L. meridionalis* (54.0) and of *L.*

tridentata (67.8) and *L. hubbsi* (55.5) (Vladykov and Kott 1979a).

Although it should be noted that in all the above cases the nonparasitic lamprey clearly has a reduced number of trunk myomeres compared with the ancestral parasitic form, no marked differences were found in the paired species of *Ichthyomyzon*, *Eudontomyzon*, and *Mordacia* (Hubbs and Trautman 1937; Zanandrea 1959a; Potter et al. 1968a). The difference between the numbers of trunk myomeres in the members of a pair thus varies markedly, a feature which probably reflects differences in the times when the different nonparasitic species evolved.

Several studies have shown that the evolution of the nonparasitic habit has been accompanied by a reduction in the size and the sharpness of the teeth (see Hubbs and Potter 1971; Hardisty and Potter 1971b). The fact that at no stage during postlarval life do nonparasitic lampreys possess teeth that are either as sharp or as large as those exhibited by the fully metamorphosed representatives of their parasitic ancestors is supported by the recent investigation of metamorphosis in *L. fluviatilis* and *L. planeri* (Bird and Potter 1979b). Rather surprisingly, however, an examination of the oral disc of *L. planeri* has shown that this nonparasitic lamprey has a greater number of teeth than *L. fluviatilis*, both in the anterior field and in the marginal rows of the lateral and posterior fields (Hardisty et al. 1970). A similar situation has been found in *Mordacia*, with the nonparasitic species containing more radial tooth plates on the oral disc and a greater number of cusps on the infraoral lamina (Potter et al. 1968a). Similarly, in the three paired species of *Ichthyomyzon*, there is an overall trend towards an increase in the number of teeth, and in the number of cusps on the supraoral, circumorals, and infraoral lamina. Thus, the lowest numbers are found in *I. unicuspis*, which attains the largest body size and is believed to be the most primitive parasitic species, whereas the greatest numbers are present in *I. greeleyi*, the nonparasitic derivative of the smallest and most advanced of the parasitic species (Hubbs and Trautman 1937; Hubbs and Potter 1971). The reverse trend, i.e. a decrease in numbers of teeth, is found in the nonparasitic *L. folletti*, *L. hubbsi*, and *L. lethophaga* compared with the situation in *L. tridentata* from which they may all have been ultimately derived (Hubbs 1971; Vladykov and Kott 1976b, c). A reduction in the number of oral disc teeth has also occurred in the evolution of *Eudontomyzon vladykovi* from *E. danfordi* (Zanandrea 1959a). The smallest number of intermediate teeth in the anterior field of any lamprey is found in what is now tentatively called *L. aepyptera* (see species list). In this latter case, the representatives of the population studied by Hubbs and Potter (1971) were so degenerate that these workers tentatively placed this species in the genus *Okkelbergia*, a position which, on the basis of the specimens they examined, Vladykov and Kott (1976a) regard as invalid.

It has been suggested by Hubbs and Potter (1971) that the variable degree of difference between the dentition of ancestral and derivative species reflects the repeated evolution of nonparasitic lampreys at different times. Such a view would be consistent with the variation in the number of trunk myomeres between members of a pair reported earlier. In the context of dentition, it seems reasonable to assume that the lampreys with the most reduced dentition are of the greatest antiquity. The evolution of nonparasitic lampreys has thus apparently involved an initial increase in the number of teeth and cusps in certain tooth series, followed by an overall reduction in the components of the dentition. While this trend is presumably related to the loss of the parasitic mode of feeding, the concomitant decline in trunk myomere number may be associated with the overall marked decrease in the body length attained at sexual maturity. Although the numbers of teeth in some series are greater in what are believed to be the most recently evolved of the nonparasitic lampreys, studies on both *Lampetra* and *Mordacia* have shown that variability in number also increases in the nonparasitic species (Potter et al. 1968a; Hardisty et al. 1970). This has been taken by Hardisty and Potter (1971b) to suggest a reduction in those selection pressures which in parasitic forms would tend to stabilize the functional arrangement of the teeth.

The above morphological data provide strong indications that nonparasitic lampreys have evolved at different times and that certain characters in these species undergo quantitative changes with time. Such features can be related to the proliferation in the number of nonparasitic species that have been described within certain taxa during the last few years. Thus, the different nonparasitic species in both the subgenera *Entosphenus* and *Lethenteron* (see species list), which may be distinguished by differences in such characters as numbers of teeth and trunk myomeres, may all have been derived at different times, and often also in different localities from *L.* (*E.*) *tridentata* in the first case and *L.* (*Le.*) *japonica* in the second. If this is indeed the case, the species validity of these nonparasitic lampreys may be questionable.

CHROMOSOME AND ELECTROPHORETIC STUDIES

The chromosome numbers of representatives of three genera of petromyzonids are very similar (Robinson et al. 1974). For this reason, it is not surprising to discover therefore that in the only investigation of the chromosomes of paired species, the modal diploid number of both *L. fluviatilis* and *L. planeri* was 164 and that their respective chromosomal areas of 167 and 162 μm^2 were very similar (Robinson et al. 1974). The similarity in chromosomal composition is paralleled by the situation with nuclear DNA content in which the respective values correspond to 41.3 and 40.5% of the amount found in the female human leucocyte (Robinson et al. 1975). The diploid number of the nonparasitic *M. praecox* was also identical with that of its presumed ancestor *M. mordax* (Potter et al. 1968b; Robinson and Potter 1969). Although the diploid number for these two species was only 76, it is worth noting that the DNA values for *M. mordax* were 40.7% of that found in the female human leucocyte and therefore very similar to the values obtained for the paired species of *Lampetra* discussed above. From the limited data obtained thus far, it would seem reasonable to assume that a study of chromosomal composition is not likely to produce a method for discriminating between the members of any paired species.

Comparatively few electrophoretic studies have been carried out on paired species. Moreover, in any attempt to contrast the proteins of one lamprey with another, it is important to recognize that these often undergo considerable changes during metamorphosis. Comparisons between *L. fluviatilis* and *L. planeri* and between *M. mordax* and *M. praecox* have shown that, although there are generic and life cycle differences, the hemoglobin electropherograms of the larvae in each paired species are identical and the same is also true for the adults (Adinolfi et al. 1959; Potter and Nicol 1968; Potter and Brown 1975). The similarity between biochemical characters of the members of paired species emphasizes the close phylogenetic relationship between certain parasitic and nonparasitic species.

DURATION OF LARVAL LIFE AND SIZE AT METAMORPHOSIS

Length–frequency curves obtained by Hardisty and Huggins (1970) for samples of *L. fluviatilis* from the River Teme have provided useful data for estimating the average duration of larval life in the European river lamprey. In curves constructed for a sample taken in July 1968, just prior to the onset of metamorphosis, the early immigrants of the 0+ class are represented by only a small number of animals. By contrast, very well-defined modes can be seen at about 40 and 70 mm, which correspond to the I+ and II+ year-classes. The fourth mode present in early July is still found in August/September at ~100 mm, which is very similar to the modal length of the early stages in metamorphosis caught in August and September. It is thus suggested that in early July, the animals responsible for producing this mode consist of two groups, the first of which represents the III+ year-class, which will usually wait for a further year before entering metamorphosis. The second group is considered as consisting of animals predominantly of the IV+ year-class, that would have entered metamorphosis in late July or early August of 1968. The view that this latter group contains only a small number of animals greater than 4 yr old is based on the relatively large number of metamorphosing animals caught in August and September. Ammocoetes of *L. fluviatilis* thus spend 1 yr in the River Teme during which they exhibit little or no increase in length. Bearing in mind that spawning occurs in the spring and that transformation is initiated in the summer, the "average" duration of larval life in this river lamprey population is thus believed to be 4¼ yr.

There is an abundance of data to show that *L. fluviatilis* metamorphoses at a shorter length than *L. planeri* (see Hardisty and Potter 1971c). Thus, mean lengths of ~100 mm have been found in metamorphosing individuals and downstream migrants caught at various times in a number of different British river systems (Hardisty and Huggins 1970; Hardisty and Potter 1971c; Potter and Huggins 1973; Bird and Potter 1979a). Although the mean lengths of metamorphosing and adult *L. planeri* in the UK show a greater degree of variability, the range in mean lengths generally falls between 110 and 160 mm (Hardisty 1961a; Hardisty and Potter 1971c; Bird and Potter 1979a). Although the growth rates vary between species, there can be little doubt that the larger length of *L. planeri* than *L. fluviatilis* at the beginning of metamorphosis represents a longer larval life in the nonparasitic species. Such a view is consistent with Hardisty's (1961a) extensive length–frequency information for *L. planeri* and with data obtained in August and September 1969 from the River Usk (Hardisty and Potter 1971c), which are characteristic of those found in many populations of this species collected from relatively stable ammocoete beds. Thus, well-defined modes were present in the River Usk data representing the 0+, I+, III+, IV+, and V+ year-classes. Moreover, the consistent spacing of these modes indicates that the slight bimodality at about 90 mm corresponds to the II+ animals. The rate of growth during the early years of larval life in *L. planeri* thus corresponds closely to that found in *L. fluviatilis* in the River Teme (Hardisty and Huggins 1970; Hardisty and Potter 1971c). The mode for metamorphosing *L. planeri* lies at almost exactly the same point as that which was designated as V+. Thus, since spawning occurs in late March and early April, and transformation generally begins in July, the average length of larval life in *L. planeri* is 6¼ yr. While the greater degree of variability found in the size of the brook than that of the river lampreys at metamorphosis may reflect the type of variation that would be expected in a longer larval phase, it may also represent a greater variation in the timing of metamorphosis and in differences between sexes (see Potter 1980). Moreover, it must be remembered that estimates based on length–frequency curves provide only average values for the duration of larval life.

The view that nonparasitic species have a longer larval phase than their parasitic counterparts is given further weight by the fact that in the Moruya River, Australia, the nonparasitic *M. praecox* metamorphoses at a significantly longer length than the parasitic *M. mordax* (Potter 1968; 1970). Moreover, in an earlier review of paired species Hardisty and Potter (1971b) suggested that there was good evidence that a similar situation existed in the *L. tridentata*/*L. lethophaga* and *L. japonica*/*L. reissneri* pairs.

DURATION OF ADULT LIFE

Information on the duration of the adult phase in the life cycle of anadromous parasitic lampreys is limited. It is clear, however, from studies on landlocked populations that adult lampreys can grow at an extremely rapid rate. For example, in the Great Lakes, *P. marinus* increased from weight and lengths of ~16 g and 190 mm to 150 g and 400 mm in a period of 7 mo (Applegate 1950). The large variation in size of different populations of *L. fluviatilis* caught at the beginning of their upstream migration in the autumn suggests that growth in this species is variable. However, data on the lengths and gonadal status of *L. fluviatilis* collected from the Gulf of Gaeta by Zanandrea (1959a) have indicated that the parasitic phase is ~1½ yr (Hardisty and Potter 1971a). This period has also been suggested as applying to British populations of the typical form of *L. fluviatilis* (Hardisty and Potter 1971b; Abou Seedo and Potter 1979). In general, the whole of the postlarval period in the life cycle of nonparasitic lampreys, including metamorphosis, sexual maturation, and spawning, lasts for between 6 and 10 mo.

DURATION OF LIFE CYCLE

From the above data, the life cycle of typical forms of *L. fluviatilis* consists of a larval life of 4¼ yr, a nontrophic period of 4–8 mo after the onset of metamorphosis (Bird and Potter 1979a, b), an adult trophic phase of about 1½ yr, and a spawning run of about 6 mo (Abou-Seedo and Potter 1979). Thus, the total life cycle occupies 7 yr with the postlarval period occupying just over 2½ yr, a time equivalent to that shown by Sterba (1969) in his diagrammatic representation of this phase in the life cycle of the river lamprey. A life cycle of 7 yr in *L. fluviatilis* is the same as that estimated for *L. planeri*, in which a larval period of about 6¼ yr is followed by a combined metamorphosing and adult period of ~9 mo (Hardisty and Potter 1971b, c). The evolution of this nonparasitic species has thus involved no change in the duration of the life cycle. It has involved, however, a change in the timing of metamorphosis, which has brought about a lengthening of the larval phase and a shortening of the adult period, the latter being accompanied by a loss of the parasitic habit.

FECUNDITY AND GONADOGENESIS

One of the major differences between the adults of closely related nonparasitic and parasitic species resides in their fecundity. Thus, mean egg counts of 15 900–34 000 for the anadromous parasitic *L. fluviatilis* contrast with values of ~1550 in *L. planeri* (Hardisty 1964; 1971). In the case of freshwater parasitic species, mean counts of 19 012 for *Ichthyomyzon unicuspis* and 7880 for *Tetrapleurodon spadiceus* may be compared with 1524 and 2215 for their respective nonparasitic derivatives, *I. fossor* and *T. geminis* (Vladykov 1951; Álvarez del Villar 1966). As can be seen from data compiled by Hardisty (1971), a similar situation exists in most of the paired species.

Histological studies have shown that the above differences can be attributed to the very extensive atresia that occurs in oocytes during the metamorphosis of nonparasitic lampreys compared with that found in any stage of postlarval life of their parasitic counterparts (Weissenberg 1927; Hardisty 1963, 1964, 1971; Hughes and Potter 1969). However, oocyte counts in large ammocoetes have shown that, even at this stage before the onset of atresia, the number of oocytes is significantly greater in parasitic than nonparasitic species. This difference between the numbers of oocytes in larvae, which is almost certainly genetically determined (Hardisty 1971), can be used to distinguish between most of the larger female ammocoetes of *L. fluviatilis* and *L. planeri* (Hardisty 1961b). Estimates of the total number of oocytes have yielded a range of values from 10 000 to 26 000 in the river lamprey and from 5000 to 10 000 in the brook lamprey (Hardisty 1971). The degree of overlap becomes conspicuous when counts were made on sections taken from comparable regions of the body. However, even with this less laborious technique, which enables estimates to be made of relative oocyte numbers, the differences in the case of both larval *L. fluviatilis* and *L. planeri* and of the early metamorphosing stages of *M. mordax* and *M. praecox* are significant (Hardisty 1961b, 1971; Hughes and Potter 1969; Hardisty and Potter 1971b).

The differences in the number of oocytes, i.e. the potential fecundity of the ammocoete, has been related to the differences in the phasing of gonadal development. Thus, significant events in larval gonadogenesis, such as the initial onset of mitotic division in the germ cells and the initiation of oogenesis, take place a year later in *L. fluviatilis* than in *L. planeri* (Hardisty 1970). The view that the phasing of gonadal development and fecundity are related is supported by the fact that in anadromous *P. marinus*, which has a large potential fecundity, gonadogenesis is delayed much longer than in *Lampetra* spp. (Hardisty 1971). Moreover, the trend towards a reduced potential fecundity and an earlier onset of gonadogenesis observed in the evolution of *L. planeri* from *L. fluviatilis* is also detected in the evolution of the landlocked form of the sea lamprey from its anadromous counterpart (Hardisty 1969). It can thus be postulated that a high larval fecundity can probably be achieved only when gonadogenesis is delayed.

CHANGES DURING METAMORPHOSIS

Comparatively few studies have been made of the morphological changes that take place throughout the metamorphosis of the respective members of any paired species. The absence of such data can be attributed largely to the problems that have been encountered in the past in separating the larval and early metamorphosing stages of closely related lampreys. This problem has been overcome in certain cases through a greatly increased knowledge of the distribution of certain species, which has enabled allopatric populations of both nonparasitic and parasitic species to be collected.

On the basis of external characters, *L. fluviatilis* can be easily distinguished from *L. planeri* after metamorphosis has been progressing for ~4 mo (Hardisty et al. 1970). The main distinguishing features are the relatively large size of the eye and disc, and the more pronounced silver coloration of the river lamprey. Recent work using qualitative and quantitative characters has followed the sequence of postlarval changes through to the downstream migration of *L. fluviatilis* and to the assumption of sexual maturity in *L. planeri* (Bird and Potter 1979a, b). This study has confirmed that, although the trends exhibited by *L. planeri* are similar to those of *L. fluviatilis* for the first five stages of metamorphosis, which take about 2 mo to complete, the morphological patterns exhibited in the subsequent stages in the following 2 mo increasingly diverge. In stage 6 and the downstream migrant (stage 7) of the river lamprey, the oral disc and lingual teeth continue to develop markedly, the eye enlarges further, and the silver coloration becomes more enhanced. In contrast to these changes, which are adaptations to a marine predatory existence, the comparable changes in the brook lamprey are less extreme, and during stages 6 and 7 the animal starts instead to develop certain of the characteristics displayed by the river lamprey during the early part of its migration to upstream spawning grounds. In this context, it is almost certainly of significance that a very marked enlargement and development of the gonads starts at stage 5.

The concept that after the completion of larval life the pattern of development in nonparasitic species initially follows closely that pursued by the metamorphosing representatives of its parasitic ancestor and then changes rapidly to produce a form similar to that of the immature nontrophic upstream migrant is supported by recent studies on changes in the skin (Lethbridge and Potter 1980). Thus, for example, whereas the number of granular cells in the epidermis increased progressively through each stage of metamorphosis in *L. fluviatilis*, they started to decline in *L. planeri* after stage 5. Slightly more delayed but similar trends were found in the numbers of club cells in the epidermis and in the thickness of the collagen layer lying beneath the epidermis.

The studies of Bird and Potter (1979a, b) indicate that the rate of somatic changes during the first 2–3 mo of metamorphosis may be slower in the brook than the river lamprey. More concrete evidence that some changes at least are slowed down for an even longer period in *L. planeri*, despite the fact that it is starting to assume the gonadal and external morphological characters typical of the upstream migrants of the parasitic species, is provided by the rate of change over from the larval to adult condition in both the hemoglobins (Potter and Brown 1975) and in the sites where hemopoiesis takes place (Percy and Potter 1977). For example, whereas the larval hemoglobins had virtually been completely lost by January in *L. fluviatilis*, they were still clearly represented at the same time in *L. planeri* (Potter and Brown 1975). In the case of hemopoietic sites, the comparison can be drawn between the presence of stem cells in the intertubular tissue of the nephric fold until October in *L. planeri* but only until late August in *L. fluviatilis*.

The above results are perhaps rather unexpected in view of the rapidity with which gonadal maturation takes place during the last few months of life in *L. planeri*. However, it would appear feasible that a longer retention of some larval characters in *L. planeri* might be of advantage to a nonparasitic lamprey. Such a view is based on the fact that the burrowing habit is maintained through metamorphosis until just before spawning in the following late March or April. By contrast, within the same period, *L. fluviatilis* would either have started to spend time in coarser substrates, lying between pebbles, or have departed to the sea (Potter and Huggins 1973; Bird and Potter 1979b). Since larval blood has a greater affinity for oxygen than adult blood (Bird et al. 1976), the retention of larval hemoglobins would be of advantage to a metamorphosing and young adult *L. planeri* burrowing in a substrate composed of fine particles in which the amount of available oxygen may be restricted.

One important feature to emerge from studies on the pattern of gonadal development in *Mordacia* and *Lampetra* is that the gonads of nonparasitic and parasitic species are of a very similar size and stage of development at the onset of metamorphosis (Hughes and Potter 1969; Hardisty and Potter 1971b). For example, at this time, mean oocyte diameters of 67.8 and 90.1 μm have been recorded for *M. mordax* and *M. praecox*, respectively, and similar values of 106.4 and ~120 μm have been obtained for *L. fluviatilis* and *L. planeri*, respectively. The oocytes were thus very approximately only $\frac{1}{10}$ of the size of the mature egg (Hardisty and Potter 1971b) and in each case the cytoplasm was intensely basophilic.

Body Size and Ecology

The preceding account has emphasized the close similarity in the morphology, karyology, and hemoglobin electrophoretic patterns of the members of individual paired species. Further evidence for such an affinity is provided by the fact that hybridization between nonparasitic and parasitic lampreys has been accomplished many times in the laboratory, with the resulting larvae in some cases being maintained in aquaria for over a year (Weissenberg 1925; Enequist 1937; Cotronei 1942; Hardisty and Potter 1971b). The strong evidence for the presence of a very similar genetic constitution in the representatives of each paired species raises the question of how hybridization might be prevented under natural conditions. In this context, it is of value to consider the differences in the body size of mature adults and the type of localities where breeding takes place.

As mentioned earlier, lampreys increase in body length and weight at a very fast rate during the adult phase, even if it is restricted to only a few of the warmer months of the year. Thus, since breeding is highly seasonal, it follows that any reduction in the length of the parasitic phase, or its elimination, will result in a marked reduction in the size of the mature adults. It is for this reason that, for example, the spawning stage of the typical form of *L. fluviatilis* is generally at least twice the length of *L. planeri* (Hardisty 1961c; Hardisty and Potter 1971a; Abou-Seedo and Potter 1979). Moreover, even the "praecox" forms of the river lamprey, which are believed to feed for one summer less than the typical forms, attain a considerably greater size than the nonparasitic brook lampreys (Abou-Seedo and Potter 1979). It has been postulated that the difference in the body size of mature nonparasitic and parasitic species helps to prevent the successful breeding of river and brook lampreys (Hardisty and Potter 1971b). Such a view is based on the observation that the spawning act is dependent on the application of pressure by the male on the female and a precise positioning of the genital apparatus of the two sexes. Thus, egg extrusion and fertilization only occurs when animals of similar size are involved.

In some cases the possible hybridization of nonparasitic with parasitic lampreys is precluded by their distribution. For example, *L. aepyptera* occur in areas which do not contain any possible ancestral parasitic species. Moreover, there is evidence that, even when species occur in the same geographical region, one of the members of the pair tend to occur alone in certain rivers. This is certainly the case with *L. planeri* which is found in many small streams in the UK where *L. fluviatilis* is not present. Furthermore, there is also now abundant information to suggest that even where or if both brook and river lampreys are found in the same system, some habitats contain entirely, or almost entirely just one species. This feature is almost certainly attributable to the fact that *L. planeri* tends to prefer smaller streams for breeding whereas the spawning of *L. fluviatilis* occurs in deeper and wider areas of water. Although on a few occasions *L. fluviatilis* and *L. planeri* have been seen in the same spawning sites, they have not been observed breeding together in such situations (Huggins and Thomson 1970), a feature which is probably attributable to the problems of differences in body lengths mentioned earlier. In other words, a combination of differences in body length and their effect on spawning behavior and differences in the preference for certain spawning areas limits the opportunities of *L. planeri* and *L. fluviatilis* interbreeding.

The data presented in this review, and in those of Hardisty and Potter (1971b, c), show that the evolution of nonparasitic lampreys has not involved a great change in the duration of the life cycle. It has involved, however, a change in the time at which metamorphosis occurs, with the result that larval life has been extended and the adult phase shortened. The reduction of the adult period to less than 1 yr has led to the loss of the parasitic habit. This marked reduction in the duration of postlarval life has not been accompanied, however, by a marked acceleration of gonadal development in the ammocoete. Most of the ovarian and testis growth thus occurs in the terminal few months of life.

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Abou-Seedo, F. S., and I. C. Potter. 1979. The estuarine phase in the spawning run of the River lamprey (*Lampetra fluviatilis*). J. Zool. (London) 188: 5–25.

Adam, H., and R. Strahan. 1963. Systematics and geographical distribution of myxinoids, p. 1–8. *In* A. Brodal and R. Fänge [ed.] The biology of *Myxine*. Universitetsforlaget, Oslo.

Adinolfi, M., G. Chieffi, and M. Siniscalco. 1959. Haemoglobin pattern of the cyclostome during the course of development. Nature, London 184: 1325–1326.

Álvarez del Villar, J. 1966. Ictiología michoacana, IV. Contribución al conocimiento biológico y sistemático de las lampreas de Jacona, Mich., México. An. Esc. Nac. Cienc. Biol. Mex. 13: 107–144.

Applegate, V. C. 1950. Natural history of the sea lamprey, *Petromyzon marinus*, in Michigan. Spec. Sci. Rep. U.S. Wildl. Serv. Fish. 55: 237 p.

Bagenall, T. B. 1973. Identification of British Fishes. Hulton, Amersham.

Bardack, D., and R. Zangerl. 1968. First fossil lamprey: a record from the Pennsylvanian of Illinois. Science 162: 1265–1267.

1971. Lampreys in the fossil record, p. 67–84. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. I. Academic Press, London.

Beamish, F. W. H. 1980. Biology of the North American anadromous sea lamprey, *Petromyzon marinus*. Can. J. Fish. Aquat. Sci. 37: 1924–1943.

Beamish, F. W. H., P. D. Strachan, and E. Thomas. 1978. Osmotic and ionic performance of the anadromous sea lamprey, *Petromyzon marinus*. Comp. Biochem. Physiol. 60A: 435–443.

Beamish, R. J. 1980. Adult biology of the river lamprey (*Lampetra ayresi*) and the Pacific lamprey (*Lampetra tridentata*) from the Pacific coast of Canada. Can. J. Fish. Aquat. Sci. 37: 1906–1923.

Berg, L. S. 1931. A review of the lampreys of the northern hemisphere. Ezheg. Zool. Muz. 32: 87–116.

1933. Die bipolare Verbreitung der Organismen und die Eiszeit. Zoogeographica 1: 449–484.

1940. Classification of fishes both recent and fossil. [In Russian]. Trudy Zool. Inst. Leningr. 5: 87–517. English translation 1947. Ann Arbor, Michigan: Edwards.

1948. Freshwater fishes of the USSR and adjacent countries. Acad. Sci. USSR. Zoological Institute: Guide to the Fauna of the USSR, No. 27 (Transl. from Russian by Israel Program for Sci. Transl., Jerusalem, 1950).

Bird, D. J., P. L. Lutz, and I. C. Potter. 1976. Oxygen dissociation curves of the blood of larval and adult lampreys (*Lampetra fluviatilis*). J. Exp. Biol. 65: 449–458.

Bird, D. J., and I. C. Potter. 1979a. Metamorphosis in the paired species of lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). 2. Quantitative data for body proportions, weights, lengths and sex ratios. J. Linn. Soc. London Zool. 65: 145–160.

1979b. Metamorphosis in the paired species of lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). 1. A description of the timing and stages. J. Linn. Soc. London Zool. 65: 127–143.

Cotronei, G. 1942. Esperienze d'ibridazione nei Petromizonti. Pubbl. Staz. Zool. Napoli. 19: 71–88.

Creaser, C. W., and C. L. Hubbs. 1922. A revision of the holarctic lampreys. Occ. Pap. Mus. Zool. Univ. Mich. 120: 1–14.

De Buen, F. 1961. Las lampreas (Marsipobranchii o Ciclostomi) en aguas de Chile. Investnes Zool. Chil. 7: 101–124.

Dohi, Y., Y. Sugita, and Y. Yoneyama. 1973. The self-association and oxygen equilibrium of hemoglobin from the lamprey, *Entosphenus japonicus*. J. Biol. Chem. 248: 2354–2363.

Eddy, J. M. P. 1972. The pineal complex, p. 91–103. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2. Academic Press, London.

Eigenman, C. H. 1928. The fresh-water fishes of Chile. Mem. Natn. Acad. Sci. 22: 1–80.

Enequist, P. 1937. Das Bachneunauge als ökologische Modification des Flusseneunauges. Über die Fluss — und Bachneunaugen Schwedens. Ark. Zool. 29: 1–22.

Fontaine, M. 1958. Classe des Cyclostomes. Formes actuelles superordres des Petromyzonoidea et des Myxinoidea, p. 13–172. *In* P. Grassé [ed.] Traité de Zoologie 13, Masson, Paris.

Fowler, H. W. 1940. Fishes obtained in Chile by Mr. B. S. Bullock. Proc. Acad. Nat. Sci. Philadelphia 92: 171–190.

Gill, T. 1893. Families and sub-families of fishes. Mem. Natn. Acad. Sci. 6: 125–128.

Hardisty, M. W. 1961a. The growth of larval lampreys. J. Anim. Ecol. 30: 357–371.

1961b. Oocyte numbers as a diagnostic character for the identification of ammocoete species. Nature, London 191: 1215–1216.

1961c. Studies on an isolated spawning population of the brook lamprey (*Lampetra planeri*). J. Anim. Ecol. 30: 339–355.

1963. Fecundity and speciation in Lampreys. Evolution 17: 17–22.

1964. The fecundity of lampreys. Arch. Hydrobiol. 60: 340–357.

1969. A comparison of gonadal development in the ammocoete of the landlocked and anadromous forms of the sea lamprey, *Petromyzon marinus* L. J. Fish. Biol. 1: 153–166.

1970. The relationship of gonadal development to the life cycles of the paired species of lamprey, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). J. Fish. Biol. 2: 173–181.

1971. Gonadogenesis, sex differentiation and gametogenesis, p. 295–359. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. I. Academic Press, London.

1979. The Cyclostomes. Chapman and Hall, London.

Hardisty, M. W., and R. J. Huggins. 1970. Larval growth in the river lamprey, *Lampetra fluviatilis*. J. Zool. London 161: 549–559.

Hardisty, M. W., and I. C. Potter. 1971a. The general biology of adult lampreys, p. 127–206. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. I. Academic Press, London.

1971b. Paired species, p. 249–277. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. I. Academic Press, London.

1971c. The behaviour, ecology and growth of larval lampreys, p. 85–125. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. I. Academic Press, London.

Hardisty, M. W., I. C. Potter, and R. Sturge. 1970. A comparison of the metamorphosing and macrophthalmia stages in the lampreys, *Lampetra fluviatilis* and *L. planeri*. J. Zool. (London) 162: 383–400.

Heintz, A. 1963. Phylogenetic aspects of myxinoids, p. 9–21. *In* A. Brodal and R. Fänge [ed.] The biology of *Myxine*. Universitets-forlaget, Oslo.

Hochachka, P. W., and G. N. Somero. 1973. Temperature, p. 179–270. *In* P. W. Hochachka and G. N. Somero [ed.] Strategies of biochemical adaptation. W. B. Saunders, Philadelphia.

Holly, M. 1933. Cyclostomata. Tierreich Lfg. 59: 1–62.

Hubbs, C. L. 1925. The life cycle and growth of lampreys. Pap. Mich. Acad. Sci. 4: 587–603.

1947. Cyclostomata or marsipobranchii. Encyclopedia Britannica 6: 921–922B.

1952. Antitropical distribution of fishes and other organisms. *In* Symposium on problems of bipolarity and of pantemperate faunas. Proc. Pacif. Sci. Congr. 7: 324–329.

1971. *Lampetra* (*Entosphenus*) *lethophaga*, new species, the nonparasitic derivative of the Pacific Lamprey. Trans. San Diego Soc. Nat. Hist. 16: 125–164.

Hubbs, C. L., and I. C. Potter. 1971. Distribution, phylogeny and taxonomy, p. 1–65. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. I. Academic Press, London.

Hubbs, C. L., and M. B. Trautman. 1937. A revision of the lamprey genus *Ichthyomyzon*. Misc. Publ. Mus. Zool. Univ. Mich. 35: 109 p.

Huggins, R. J., and A. Thompson. 1970. Communals pwaning of brook and river lampreys, *Lampetra planeri* Bloch and *Lampetra fluviatilis* L. J. Fish. Biol. 2: 53–54.

Hughes, R. L., and I. C. Potter. 1969. Studies on gametogenesis and fecundity in the lampreys *Mordacia praecox* and *M. mordax* (Petromyzonidae). Aust. J. Zool. 17: 447–464.

Ivanova-Berg, M. M. 1962. O lichinkakh minog. (On lamprey larvae). Vop. Ikhtiol. 2: 557. (In Russian)

1968. Discovery of the Southern Lamprey (*Geotria australis* Gray) in the Scotia Sea near Georgia Island. Probl. Ichthyol. 8: 138–141.

Lanzing, W. J. R. 1957. Biologie van de Petromyzonidae. Vakbl. Biol. 37: 1–10.

Lethbridge, R. C., and I. C. Potter. 1979. The oral fimbriae of the lamprey *Geotria australis*. J. Zool. London 188: 267–277.

1980. Quantitative studies on the skin of the paired species of lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). J. Morphol. 164: 39–46.

MacDonald, T. H. 1959. Identification of ammocoetes of British lampreys. Glasgow Nat. 18: 91–95.

Macey, D. J., and I. C. Potter. 1978. Lethal temperatures of ammocoetes of the Southern Hemisphere lamprey, *Geotria australis* Gray. Env. Biol. Fish. 3: 241–243.

Maitland, P. S. 1972. A key to the freshwater fishes of the British Isles. Freshwater Biol. Ass. Sci. Publ. 27: 139 p.

Manion, P. J., and T. M. Stauffer. 1970. Metamorphosis of the landlocked sea lamprey, *Petromyzon marinus*. J. Fish. Res. Board Can. 27: 1735–1746.

Maskell, F. G. 1929. On the New Zealand lamprey, *Geotria australis* Gray. 1. Biology and life history. Trans. N.Z. Inst. 60: 167–201.

1930. On the New Zealand lamprey *Geotria australis* Gray. On the mid-gut diverticula, the bile duct and the problem of the pancreas in the ammocoetes stage. Trans. N.Z. Inst. 61: 478–497.

Mathers, J. S., and F. W. H. Beamish. 1974. Changes in serum osmotic and ionic concentrations in landlocked *Petromyzon marinus*. Comp. Biochem. Physiol. 49A: 677–688.

McCulloch, A. R. 1929. A check-list of the fishes recorded from Australia. Mem. Aust. Mus. 5: 1–144.

Nikolskii, G. V. 1954. Special Ichthyology. (Transl. from Russian by Israel Program for Sci. Publ., Jerusalem, 1961)

Ogilby, J. D. 1896. A monograph of the Australian Marsipobranchii. Proc. Linn. Soc. N.S.W. 21: 388–426.

Percy, R. C., and I. C. Potter. 1977. Changes in haemopoietic sites during the metamorphosis of the lampreys *Lampetra fluviatilis* and *Lampetra planeri*. J. Zool. London 183: 111–123.

Permitin, Yu. E. 1966. Some new data in specific composition and distribution of fish in the Sea of Scotia. Vop. Ikhtiol. 6: 424–431. (In Russian)

Poltorykhina, A. N. 1974. Morphological characteristics and variability of the Siberian lamprey (*Lampetra japonica* *kessleri*) from the upper Irtysh Basin. J. Ichthyol. 14: 192–202.

Potter, I. C. 1968. *Mordacia praecox*, n. sp., a nonparasitic lamprey (Petromyzonidae) from New South Wales, Australia. Proc. Linn. Soc. N.S.W. 92: 254–261.

1970. The life cycles and ecology of Australian lampreys of the genus *Mordacia*. J. Zool. London 161: 487–511.

1980. Ecology of larval and metamorphosing lampreys. Can. J. Fish. Aquat. Sci. 37: 1641–1657.

Potter, I. C., and F. W. H. Beamish. 1975. Lethal temperatures in ammocoetes of four species of lampreys. Acta Zool. (Stockholm) 56: 85–91.

Potter, I. C., and I. D. Brown. 1975. Changes in haemoglobin electropherograms during the life cycle of two closely related lampreys. Comp. Biochem. Physiol. 51B: 517–519.

Potter, I. C., R. W. Hilliard, and D. J. Bird. 1980. Metamorphosis in the Southern Hemisphere lamprey, *Geotria australis*. J. Zool. London 190: 405–430.

Potter, I. C., and R. J. Huggins. 1973. Observations on the morphology, behaviour and salinity tolerance of downstream migrating river lampreys (*Lampetra fluviatilis*). J. Zool. London 169: 365–379.

Potter, I. C., W. J. R. Lanzing, and R. Strahan. 1968a. Morphometric and meristic studies on populations of Australian lampreys of the genus *Mordacia*. J. Linn. Soc. London Zool. 47: 533–546.

Potter, I. C., and P. I. Nicol. 1968. Electrophoretic studies on the haemoglobins of Australiam lampreys. Aust. J. Exp. Biol. Med. Sci. 46: 639–641.

Potter, I. C., and T. S. Osborne. 1975. The systematics of British larval lampreys. J. Zool. London 176: 311–329.

Potter, I. C., P. A. Prince, and J. P. Croxall. 1979. Data on the adult marine and migratory phases in the life cycle of the Southern Hemisphere lamprey, *Geotria australis* Gray. Environ. Biol. Fish. 4: 65–69.

Potter, I. C., E. S. Robinson, and S. M. Walton. 1968b. The mitotic chromosomes of *Mordacia mordax* (Agnatha: Petromyzonidae). Experientia 24: 966–967.

Potter, I. C., and R. Strahan. 1968. The taxonomy of the lampreys *Geotria* and *Mordacia* and their distribution in Australia. Proc. Linn. Soc. London 179: 229–240.

Potter, I. C., G. M. Wright, and J. H. Youson. 1978. Metamorphosis in the anadromous sea lamprey, *Petromyzon marinus* L. Can. J. Zool. 56: 561–570.

Prosser, C. L. 1973. Temperature, p. 362–419. *In* C. L. Prosser [ed.] Comparative animal physiology. W. B. Saunders, Philadelphia.

Raney, E. C. 1952. A new lamprey, *Ichthyomyzon hubbsi*, from the upper Tennessee River system. Copeia 1952: 95–99.

Rauther, M. 1924. Cyclostomi. Bronn's Kl. Ordn. Tierreichs 6: 250–703.

Regan, C. T. 1911. A synopsis of the marsipobranchs of the order Hyperoartii. Ann. Mag. Nat. Hist. (8)7: 193–204.

Reynolds, W. M., and M. E. Casterlin. 1978. Behavioural thermoregulation by ammocoete larvae of the sea lamprey (*Petromyzon marinus*) in an electronic shuttlebox. Hydrobiologia 61: 145–147.

Robinson, E. S., and I. C. Potter. 1969. Meiotic chromosomes of *Mordacia praecox* and a discussion of chromosome numbers in lampreys. Copeia 1969: 824–828.

Robinson, E. S., I. C. Potter, and N. B. Atkin. 1975. The nuclear DNA content of lampreys. Experientia 31: 912–913.

Robinson, E. S., I. C. Potter, and C. J. Webb. 1974. Homogeneity of holarctic lamprey karyoptypes. Caryologia 27: 443–454.

Scott, T. D. 1962. The marine and freshwater fishes of South Australia. Government Printer, Adelaide.

Smith, B. R. 1971. Sea lampreys in the Great Lakes of North America, p. 207–247. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. I. Academic Press, London.

Sterba, G. 1969. Endocrinology of the lampreys. Gen. Comp. Endocrinol. Suppl. 2: 500–509.

Strahan, R. 1959. The status of *Yarra singularis* and *Geotria australis* (Petromyzontidae). J. Proc. R. Soc. West. Aust. 42: 49–52.

Strahan, R., and J. L. Maclean. 1969. A pancreas-like organ in the larva of the lamprey *Mordacia mordax*. Aust. J. Sci. 32: 54–55.

Vladykov, V. D. 1949. Quebec lampreys (Petromyzonidae). 1. List of species and their economical importance. Contrib. Dep. Pech. Que. 26: 67 p.

1950. Larvae of eastern American lampreys (Petromyzonidae) 1. Species with two dorsal fins. Naturaliste Can. 77: 73–94.

1951. Fecundity of Quebec lampreys. Can. Fish. Cult. 10: 14 p.

1955. *Lampetra zanandreai*, a new species of lamprey from northern Italy. Copeia 1955: 215–223.

1960. Description of young ammocoetes belonging to two species of lampreys: *Petromyzon marinus* and *Entosphenus lamottenii*. J. Fish. Res. Board Can. 17: 267–288.

1973. *Lampetra pacifica*, a new nonparasitic species of lamprey (Petromyzontidae) from Oregon and California. J. Fish. Res. Board Can. 30: 205–213.

Vladykov, V. D., and W. I. Follett. 1958. Redescription of *Lampetra ayresii* (Günther) of western North America, a species of lamprey (Petromyzonidae) distinct from *Lampetra fluviatilis* (Linnaeus) of Europe. J. Fish. Res. Board Can. 15: 47–77.

1965. *Lampetra richardsoni*, a new nonparasitic species of lamprey (Petromyzonidae) from western North America. J. Fish. Res. Board Can. 22: 139–158.

1967. The teeth of lampreys (Petromyzonidae), their terminology and use in a key to the Holarctic genera. J. Fish. Res. Board Can. 24: 1067–1075.

Vladykov, V. D., and G. C. Gruchy. 1975. Request for a ruling on the stem of the Family-group name based on the Type-genus *Petromyzon* Linnaeus, 1758: Revised application. Z.N.(S.) 2045 Bull. Zool. Nomencl. 32: 154–155.

Vladykov, V. D., and E. Kott. 1976a. Is *Okkelbergia* Creaser and Hubbs, 1922 (Petromyzonidae) a distinct taxon? Can. J. Zool. 54: 421–425.

1976b. A second nonparasitic species of *Entosphenus* Gill, 1862 (Petromyzonidae) from Klamath River System, California. Can. J. Zool. 54: 974–989.

1976c. A new nonparasitic species of lamprey of the genus *Entosphenus* Gill, 1862 (Petromyzonidae) from south central California. Bull. South. Calif. Acad. Sci. 75: 60–67.

1978a. A new nonparasitic species of the holarctic lamprey genus *Lethenteron* Creaser and Hubbs, 1922, (Petromyzonidae) from northwestern North America with notes on other species of the same genus. Biol. Pap. Univ. Alaska 19: 74 p.

1978b. A new nonparasitic species of *Lethenteron*

Creaser and Hubbs 1922 (Petromyzonidae) from Hokkaido, Japan. Can. J. Zool. 56: 1792–1800.

1979a. Satellite species among the holarctic lampreys. Can. J. Zool. 57: 860–870.

1979b. List of Northern Hemisphere lampreys (Petromyzonidae) and their distribution. Dep. Fish. Oceans, Ottawa Misc. Spec. Publ. 42.

1979c. A new parasitic species of the holarctic lamprey genus *Entosphenus* Gill, 1862 (Petromyzonidae) from Klamath River, in California and Oregon. Can. J. Zool. 57: 808–823.

Vladykov, V. D., E. Kott, and S. Pharand-Coad. 1975. A non-parasitic species of lamprey genus *Lethenteron* (Petromyzonidae), from eastern tributaries of the Gulf of Mexico, U.S.A. Nat. Mus. Canada Publ. Zool. 12: 36 p.

Waite, E. R. 1921. Illustrated catalogue of the fishes of South Australia. Rec. South Aust. Mus. (Adelaide) 2: 1–208.

Weissenberg, R. 1925. Fluss- und Bachneunauge (*Lampetra fluviatilis* L. und *Lampetra planeri* Bloch), ein morphologisch-biologischer Vergleich. Zool. Anz. 63: 293–306.

1926. Beitrage zur Kenntnis der Biologie und Morphologie der Neunaugen. 1. Vorderdarm und Mundbewaffnung bei *Lampetra fluviatilis* und *planeri*. Z. Mikrosk. Anat. Forsch. 5: 153–184.

1927. Beitrage zur Kenntnis der Biologie und Morphologie der Neunaugen. 2. Das Reifewachstum der Gonaden bei *Lampetra fluviatilis* und *planeri*. Z. Mikrosk. Anat. Forsch. 8: 193–249.

Whitley, G. P. 1932. The lancelets and lampreys of Australia. Aust. Zool. 7: 256–264.

1940. The fishes of Australia. I. The sharks, rays, devil fish, and other primitive fishes of Australia and New Zealand. Royal Zoological Society of New South Wales, Sydney. 280 p.

Wigley, R. L. 1959. Life history of the sea lamprey of Cayuga Lake, New York. U.S. Fish. Wildl. Serv. Fish. Bull. 59: 559–617.

Young, J. Z. 1950. The life of vertebrates. Clarendon Press, Oxford.

Zanandrea, G. 1957. Esame critico e comparativo delle Lamprede catturate in Italia. Arch. Zool. Ital. 42: 249–307.

1958. Posizione sistematica e distribuzione geografica di *Lampetra zanandreai* Vladykov. Mem. Mus. Civ. Stor. Nat. "G. Doria" 6: 207–237.

1959a. Lamprede parassite e non parassite nel bacino del Danubio e la nuova entita sistematica *Eudontomyzon danfordi vladykovi*. Arch. Zool. Ital. 44: 215–249.

1959b. Recenti ricerche sulle forme "appaite" di lamprede dell'Italie e del Danubio. Boll. Zool. 26: 545–554.

1959c. Speciation amongst lampreys. Nature, London 184: 386.

1959d. *Lampetra fluviatilis* catturata in mare nel Golfo di Gaeta. Pubbl. Staz. Zool. Napoli 31: 265–307.

1962. Rapporti tra continenti e isole nella biogeografia delle lamprede in Italia. Boll. Zool. 28: 529–544.

Description and Key to Metamorphosed Specimens and Ammocoetes of Petromyzonidae Found in the Great Lakes Region[1]

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VLADYKOV, V. D., AND E. KOTT. 1980. Description and key to metamorphosed specimens and ammocoetes of Petromyzonidae found in the Great Lakes Region. Can. J. Fish. Aquat. Sci. 37: 1616–1625.

At present five species of Petromyzonidae are found in the Great Lakes region. Of these, three are parasitic: *Petromyzon marinus*, *Ichthyomyzon unicuspis*, and *I. castaneus*; two are nonparasitic: *I. fossor* and *Lethenteron lamottenii*. It is quite possible that a nonparasitic sixth species, *Lampetra aepyptera*, could be found in the Lake Erie basin.

Key words: lampreys, Great Lakes, keys, *P. marinus*, abnormality, *L. lamottenii*, gigantism

VLADYKOV, V. D., AND E. KOTT. 1980. Description and key to metamorphosed specimens and ammocoetes of Petromyzonidae found in the Great Lakes Region. Can. J. Fish. Aquat. Sci. 37: 1616–1625.

On trouve présentement cinq espèces de Petromyzonidés dans la région des Grands Lacs. Trois de ces espèces sont parasites : *Petromyzon marinus*, *Ichthyomyzon unicuspis* et *I. castaneus*; deux ne le sont pas : *I. fossor* et *Lethenteron lamottenii*. Il est fort possible que l'on puisse trouver, dans le bassin du lac Érié, une sixième espèces, *Lampetra aepyptera*, qui n'est pas parasite.

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IN North America 23 species of holarctic lampreys are found (Vladykov and Kott 1979a, b). Of this number only five species have been reported from the Great Lakes Region (Hubbs and Lagler 1964). *Petromyzon marinus* is the most important. A very extensive bibliography exists on this species, especially on its destructive habits of feeding voraciously on fishes (Laurie 1970; Beamish and Potter 1975) and to a lesser degree on cetaceans (van Utrecht 1959).

A comprehensive review of the role of landlocked *P. marinus* in the Great Lakes is given by Smith (1971). Earlier authors dealing with the natural history of *P. marinus* include Applegate (1950) and Piavis (1961). Recently, Manion and Smith (1978) and Purvis (1979) have provided valuable information on the ammocoetes and their age at metamorphosis. The ability of *P. marinus* to prey successfully on fishes depends on its strong dentition and particularly on its well-developed buccal glands producing anticoagulants that prevent clotting of host blood. Descriptions of buccal glands have been given by several authors, particularly Baxter (1956) and Gibbs (1956). Information on anadromous *P. marinus* can be found in Vladykov (1949), Davis (1967), Beamish and Potter (1975), and Potter and Beamish (1977).

For other species in the Great Lakes Region, especially those of the genus *Ichthyomyzon*, consult Hubbs and Trautman (1937) and Hubbs and Lagler (1964). Hall (1963) studied *I. castaneus*; Vladykov and Roy (1948) and Roy (1973) published information on the biology of *I. unicuspis*. The following authors dealt with the life history or distribution of *I. fossor*: Leach (1940), Vladykov (1949), and Purvis (1970).

Information on morphology and distribution of *Lethenteron lamottenii* can be found in Vladykov (1949), Manion and Purvis (1971), Kott (1974), and Vladykov and Kott (1978, 1979b). Moore and Braem (1965) presented the distribution of lampreys in U.S. stream tributaries to Lake Superior, and Morman (1979) for the lower Peninsula of Michigan.

List of Species

Five species of Petromyzonidae have been reported in the Great Lakes Region (Hubbs and Lagler 1964). Because of the proximity of the Ohio River to Lake Erie (Trautman 1957) there is always the possibility

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that *Lampetra aepyptera*, a widely distributed species, could penetrate into the Lake Erie drainage. For important information on this species, see Seversmith (1953), Vladykov et al. (1975), and Rhode et al. (1976). These six species, including *L. aepyptera*, belong to two subfamilies (Fowler 1964; Vladykov 1972). To distinguish nonparasitic species from parasitic ones in the following list, the latter are preceded by (P).

Subfamily PETROMYZONINAE

1) (P) *Petromyzon marinus* Linnaeus, 1758, Atlantic sea lamprey;[2]
2) (P) *Ichthyomyzon unicuspis* Hubbs and Trautman, 1937, Northern lamprey;[3]
3) (P) *I. castaneus* Girard, 1958, Chestnut lamprey;
4) *I. fossor* Reighard and Cumming, 1916, Northern brook lamprey.

Subfamily LAMPETRINAE

5) *Lethenteron lamottenii*[4] (Le Sueur 1827), American brook lamprey;
6) *Lampetra aepyptrea* (Abbott 1860), Least brook lamprey.

Methods

MEASUREMENTS

Measurements and meristic counts were made typically on the left side of the specimen and the procedures outlined by Vladykov and Follett (1965) were followed. Measurements are expressed as percentages of the total length of the specimen.

a–C: tail length, the distance from the posterior edge of the cloacal slit to the end of the caudal fin.
B_7–a: trunk length, the distance from the posterior edge of the last (seventh) branchial opening to the anterior edge of the cloacal slit.
B_1–B_7: branchial length, the distance from the anterior edge of the first branchial opening to the posterior edge of the last (seventh) branchial opening.
d: disc length, longitudinal diameter, with the oral fimbriae included, measured with the disc closed.
d–B_1: prebranchial length, the distance from the anterior edge of the disc in transformed individuals or of the upper lip (in ammocoetes) to the anterior edge of the first branchial opening.
d–O: snout length, the distance from the most anterior point of the snout to the front of the eye.
O: eye length, the horizontal diameter of the eye.
TL: total length, the distance from the most anterior oral fimbria to the end of the caudal fin.

Metamorphosed Specimens

We follow the nomenclature of Vladykov and Follett (1967) for lamprey teeth. Differences in dentition for the six species are illustrated in Fig. 1. The use of velar tentacles in taxonomic studies has been described by Vladykov and Kott (1976).

The distinction between the subfamilies and individual species are given in the key and Table 1–4.

Key for Identification of Metamorphosed Lampreys (Petromyzonidae) from the Great Lakes Region

1 Anterials, posterials, and exolaterals (or outer laterals) numerous, close set in 3–4 curvilinear radiating rows; instead of supraroral lamina, a single supraoral tooth with 2–4 cusps not separated by a bridge; 4(5, the rare exception in *Ichthyomyzon*) endolaterals (or inner laterals) on each side of the oesophageal opening; transverse lingual lamina typically bilobed, without greatly enlarged median cusp; dorsal fins continuous (in *Ichthyomyzon*) or two fins are separated (in *Petromyzon*); median velar tentacle absent: Subfamily Petromyzoninae 2

Anterials and posterials (if present) not numerous, and not in curvilinear radiating rows; exolaterals absent; supraoral lamina with a cusp at each end, the cusps separated by a bridge (occasionally there are one or more small cusps on the middle of the bridge); 3 endolaterals on each side of the oesophageal opening; transverse lingual lamina is not bilobed but convex in front and with greatly enlarged median cusp; dorsal fins separated; median velar tentacle present: Subfamily Lampetrinae 3

Subfamily PETROMYZONINAE

2 Dorsal fins separated; teeth strong, orange (yellow only in newly metamorphosed individuals); 4 pairs of endolaterals, all bicuspid; transverse lingual lamina bilobed and strongly bent inward along a median longitudinal groove with 11–18 large cusps; 67–74 trunk myomeres; sense organs of the lateral line remain unpigmented even in fully mature individuals; spawning males, in addition to relatively long genital papilla, have large rope-like ridge extending along the back from the head to the first dorsal fin; in mature females of this and all other holarctic species genital papilla present but much shorter and barely visible from the outside; females with well-developed anal fin-like fold. Only two pincer-like velar tentacles are present. Anadromous specimens in North America up to 900 mm (Vladykov 1949); in

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[2] Called "sea lamprey" in Bailey et al. (1970).

[3] Hubbs and Trautman (1937), who described *I. unicuspis*, called it "northern lamprey." This is a very appropriate term since this species is found further north than any other *Ichthyomyzon species.* This common name matches well with the name of its nonparasitic partner which is known as "northern brook lamprey." Moreover, the metamorphosed specimens or ammocoetes of *I. unicuspis* never display silver coloration.

[4] According to Bailey et al. (1970) this species is placed in the genus *Lampetra.*

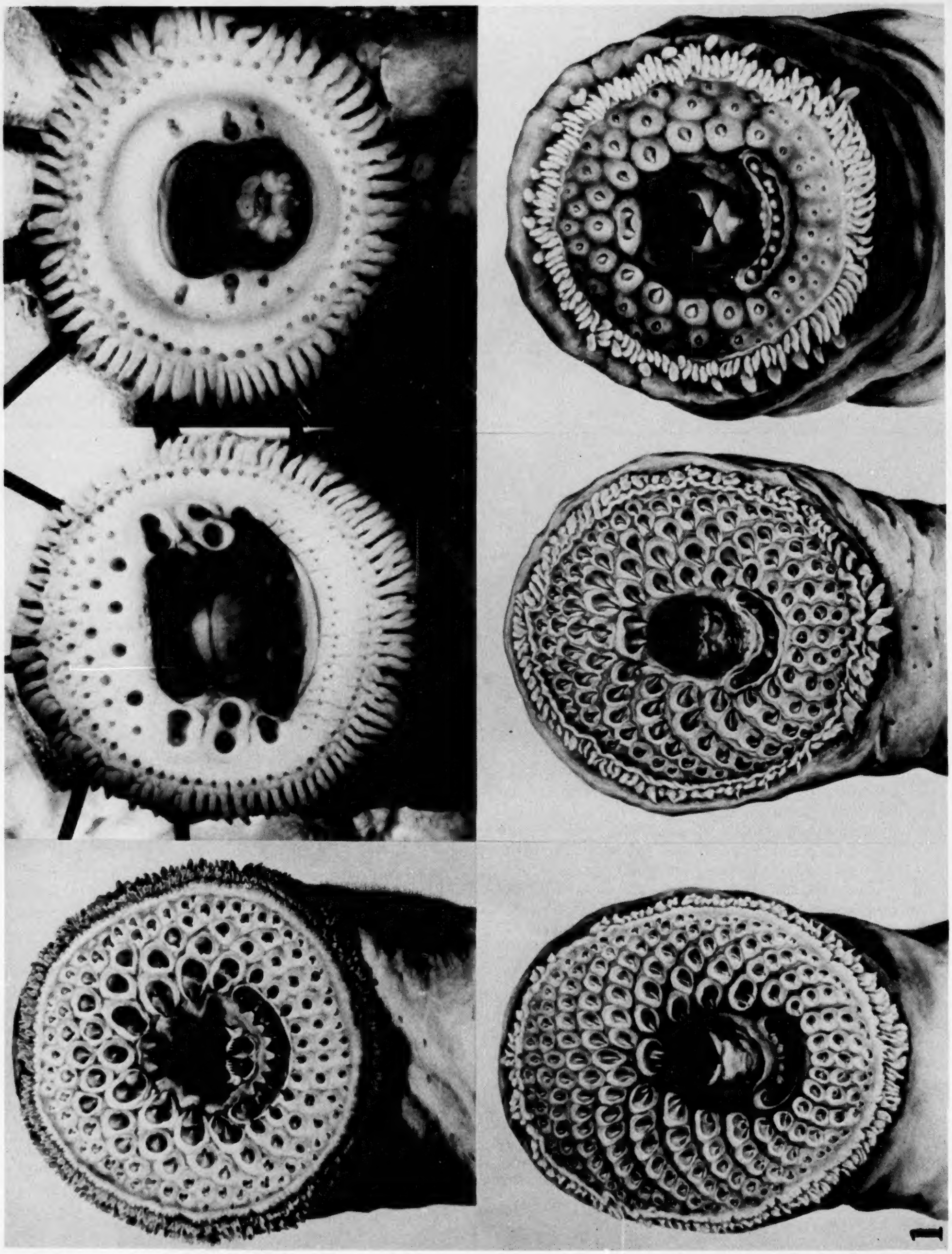

FIG. 1. Enlarged discs of lampreys from the Great Lakes Region. *Upper* row (from left to right): *Petromyzon marinus*, *Lethenteron lamottenii*, and *Lampetra aepytera*. *Lower* row: *Ichthyomyzon castaneus*, *I. unicuspis*, and *I. fossor*.

TABLE 1. Body proportions in percentage of total length in three species of *Ichthyomyzon* and other diagnostic characters. Data, taken from Hubbs and Trautman (1937), refer to means and ranges (in parentheses) for each character, sexes combined. For a definition of symbols refer to Methods.

Species	*I. unicuspis*	*I. castaneus*	*I. fossor*
TL (mm)	224 (103–328)	216 (105–310)	119 (94–146)
Trunk myomeres	50.5 (47–55)	52.6 (49–56)	50.9 (47–56)
$\frac{d\text{–}O}{TL}\%$	9.5 (7.3–13.0)	9.0 (7.5–10.9)	5.5 (4.1–6.5)
$\frac{d}{TL}\%$	8.6 (5.9–11.8)	7.7 (6.3–9.1)	4.1 (3.6–4.9)
$\frac{B_1\text{–}B_7}{TL}\%$	10.1 (8.0–12.2)	9.4 (8.3–11.4)	10.3 (9.2–11.9)
$\frac{O}{TL}\%$	1.1 (0.7–2.1)	1.1 (0.7–1.7)	1.3 (1.0–1.6)
$\frac{a\text{–}C}{TL}\%$	30.2 (25.8–35.0)	28.2 (25.0–33.5)	30.4 (28.1–33.4)
Supraoral cusps	2.0 (1–4)	2.4 (2–3)	2.0 (1–2)
Bicuspid endolaterals	0.0 (0–2)	6.5 (1–10)	0.0 (0)
Shape of transverse lingual lamina	Moderately to strongly bilobed	Usually linear or weakly bilobed	Moderately to strongly bilobed
Black pigmentation of lateral line organs (metamorphosed specimens)	Evident in specimens longer than 150 mm	Evident in all specimens	Completely lacking

Europe maximum length 1200 mm (Oliva 1953); landlocked much smaller, up to 560 mm (Kott 1971) .... *Petromyzon marinus*

Dorsal fin continuous, more or less emarginated, but never divided into two distinct fins; teeth sharp, yellow in parasitic species; 4 (exceptionally 5) endolaterals, unicuspid or bicuspid; transverse lingual lamina weakly or strongly bilobed with about 30 small cusps in parasitic species; 47–58 trunk myomeres in Great Lakes species; sucking disc wide in parasitic species and small in nonparasitic species; sense organs of the lateral line darkly pigmented or lack pigmentation; spawning males lack rope-like ridge; 2–6 (exceptionally only one tentacle in *I. fossor*) very short, stub-like velar tentacles; metamorphosed specimens of parasitic species (*I. unicuspis*, *I. castaneus*) up to 370 mm in total length; transformed specimens of nonparasitic species, as *I. fossor* remain small, less than 165 mm in total length .... *Ichthyomyzon* (see Table 1)

Subfamily LAMPETRINAE

3 Anterials rather numerous in two different sizes; unicuspid posterials present as a single row; teeth rather strong especially on the transverse lingual and infraoral laminae, yellow; no supplementary marginal teeth; 65–74 trunk myomeres; caudal fin with narrow blotch; 7.3 (5–9) velar tentacles; from 105 to 317 mm in total length .... *Lethenteron lamottenii*

Anterials few, small, and of the same size; posterials lacking; teeth weak, pale yellow; supplementary marginal teeth typically present, 50–59 trunk myomeres; caudal fin lacks black blotch; 3.5 (3–5) velar tentacles; total length smaller than 180 mm .... *Lampetra aepyptera* (see Table 2)

Ammocoetes

In earlier studies Vladykov (1950, 1960) described methods of separating larvae (ammocoetes) of lampreys with two distinct dorsal fins: ***P. marinus***, ***Lethenteron lamottenii***, and ***Lampetra aepyptera***. The usefulness of these characters was confirmed by several authors: Distler (1957), Hubbs and Lagler (1964), Potter and Osborne (1975). Because of incompleteness of material our present study of am-

TABLE 2. Body proportions (percentage of total length) in three species of lampreys with two separate dorsal fins: *Petromyzon marinus*, *Lethenthon lamottenii*, and *Lampetra aepyptera*, sexes combined. Data for *P. marinus* original; for *L. lamottenii* from Vladykov and Kott (1978); for *L. aepyptera* from Vladykov et al. (1975). For definition of symbols see Methods.

Species	*n*	Total length (mm)	$\frac{\mathrm{d}}{\mathrm{TL}}$	$\frac{\mathrm{d{-}B_1}}{\mathrm{TL}}$	$\frac{\mathrm{B_1{-}B_7}}{\mathrm{TL}}$	$\frac{\mathrm{O}}{\mathrm{TL}}$	$\frac{\mathrm{B_7{-}a}}{\mathrm{TL}}$	$\frac{\mathrm{a{-}C}}{\mathrm{TL}}$
P. marinus	24	160.8 (131–212)	10.0 (8.0–13.19)	15.5 (13.13–16.79)	10.5 (9.09–13.44)	3.4 (2.45–4.39)	46.8 (42.21–49.28)	29.2 (24.73–33.12)
	20	326.6 (281–359)	8.6 (7.07–9.61)	13.7 (12.42–16.07)	10.1 (8.19–10.82)	2.7 (2.11–3.27)	49.8 (45.66–52.08)	27.4 (24.40–31.36)
	8	422.0 (398–475)	8.6 (7.81–9.8)	14.3 (12.86–15.53)	10.6 (9.47–11.81)	2.3 (2.01–2.55)	49.5 (47.33–50.97)	27.5 (23.58–29.30)
	5	614.0 (504–680)	7.5 (7.35–7.94)	12.9 (11.33–14.07)	10.5 (9.33–11.22)	2.1 (1.89–2.38)	53.0 (50.44–56.66)	25.8 (23.73–27.20)
L. lamottenii	81	152 (102–192)	5.3 (4.0–7.2)	10.8 (9.6–12.9)	10.1 (8.5–11.2)	2.2 (1.7–2.8)	49.7 (45.5–53.8)	28.8 (24.1–32.1)
L. aepyptera	35	112 (91–151)	5.5 (4.3–6.7)	11.5 (9.2–13.4)	10.3 (8.9–11.2)	1.9 (1.4–2.1)	50.3 (46.5–54.3)	28.6 (27.3–31.4)

mocoetes of the genus *Ichthyomyzon* is less thorough.

Although populations of *I. unicuspis* and *I. fossor* can be separated on the degree of pigmentation of the head and tail region, individual specimens are less distinct since there is some overlap in these characters. This makes it difficult to assign individuals with an intermediate degree of pigmentation.

We are still studying the problem of identifying ammocoetes of *Ichthyomyzon* by investigating additional characters. In all three species of this genus that occur in the Great Lakes, the bulb of the tongue precursor has been found to be darkly pigmented and hence not important in identification. *Ichthyomyzon* species from the Great Lakes have fewer myomeres (47–56) than *P. marinus* and *L. lamottenii*, with separate dorsal fins, in which the number of myomeres varies from 66 to 74. The number of myomeres corresponds inversely with the relative widths of the myomeres: in *Ichthyomyzon* myomeres are relatively wider than those of other genera.

If we add to the above species *Lampetra aepyptera*, which has about the same number of myomeres as *Ichthyomyzon* (50–59), then the distinction between species with two separate fins and those with a single dorsal fin becomes less pronounced.

Key to the Ammocoetes (Longer than 60 mm in Total Length) from the Great Lakes Region

1 Single dorsal fin supported along its entire length with fin rays .... 2 *Ichthyomyzon*

Two separate dorsal fins (if low membrane is present between the two dorsal fins, there are no fin rays in it) 4

2 Lateral line organs with dark pigmentation; myomeres 47–56 (mean 53) ...... *I. castaneus*

Lateral line organs unpigmented; myomeres 47–56 (mean 51) 3

3 Caudal fin and head heavily pigmented .... *I. unicuspis*

Caudal fin and head weakly pigmented . . *I. fossor*

4 Myomores 50–59; prebranchial blotch present; bulb of tongue precursor pigmented; membrane of caudal fin without dark pigmentation .... *Lampetra aepyptera*

Myomeres 66–74; prebranchial blotch absent; bulb of tongue precursor pigmented or not; caudal fin membrane with dark pigment limited or extended 5

5 Branchial region pigmented almost down to branchial groove; lower half of upper lip pigmented; membrane of caudal fin almost entirely pigmented, bulb of tongue precursor unpigmented .... *Petromyzon marinus*

Wide unpigmented band above branchial groove; lower half of upper lip unpigmented; membrane of caudal fin pigmented only about notochord; bulb of tongue precursor pigmented .... *Lethenteron lamottenii*

Additional Morphological Remarks on *Petromyzon marinus*

GENERAL

It is rather surprising that there is so little information on the morphometry of metamorphosed *P. marinus* of different sizes. Some data are given by Vladykov (1949) and Beamish and Potter (1975).

TABLE 3. Comparison between selected body parts, expressed in millimetres and as a percentage of the total length of anadromous *Petromyzon marinus*. For definition of symbols see Methods.

TL (mm)	O (mm)	$\frac{O}{TL}$ %	d (mm)	$\frac{d}{TL}$ %
144	6.0	4.2	19	13.2
153	6.5	4.3	17	11.1
304	9.5	3.1	27	8.9
357	10.0	2.8	29	8.1
412	10.5	2.6	37	9.0
475	12.0	2.5	39	8.2
504	12.0	2.4	40	7.9
680	14.5	2.1	52	7.6

Here we summarize measurements of 57 anadromous *P. marinus* from Quebec, ranging from 131 to 680 mm in total length. Although these data are rather limited, they demonstrate changes in body proportions with size irrespective of sex (Table 3). Changes were noticed as follows: prebranchial length, disc length, eye length, and tail length decreased with size; the opposite is true for trunk length. On the other hand the branchial length does not vary with size. In the case of males and females of corresponding sizes, differences could be interpreted as a manifestation of sexual dimorphism: males have larger disc, eye, and tail, but shorter trunk length. However, in spite of the decrease in body proportions with size, the growth of these parts is continuous, being allometric in nature. Table 3 contains representative examples of this phenomenon.

It must be added (Table 2) that differences in body proportions of lampreys with two distinct dorsal fins exist. In addition to being much longer, *P. marinus* has a much larger disc and eyes. Details of teeth and trunk myomeres of these three species are given in Table 4.

INFRAORAL LAMINA

The morphology of infraoral lamina of *P. marinus* changes with age. Although the number of cusps on this lamina in the landlocked race does not vary with age, as observed by Vladykov and Mukerji (1961), they are of three types: normal, inclined, and rosebud. Newly metamorphosed and young lampreys, smaller than 180 mm, have the normal type of cusps. The next stage, the rosebud cusps, is typical of half-grown specimens 250–400 mm in length. In adults feeding in lakes, the predominant type is the inclined cusps. In spawning individuals normal cusps are most frequent. Lelek (1973) reported capture of a young *P. marinus* in the sea with rosebud cusps. Such changes in morphology of the infraoral lamina have not been observed in any other species of Petromyzonidae.

Spawning *P. marinus*, in addition to the functional corneous tooth sheath, has two supplementary sets of sheaths found one beneath the other. During the life span, several replacements of the corneous tooth sheaths were observed in this species. Manion and Piavis (1977) counted up to five tooth layers: one functional and four replacements on the transverse lingual lamina. The modifications of the infraoral lamina in anadromous *P. marinus* are the same as in the landlocked form.

TAIL AND ANAL FIN

One abnormality observed quite frequently in *P. marinus* is the formation of supplementary tails (Manion 1967).

In all holarctic lamprey species, spawning females develop an anal fin-like fold, which sometimes is misinterpreted as an anal fin (Young 1962). This fold plays a very important role during the spawning activities of lampreys (Hagelin 1959; Hagelin and Steffner 1958).

The absence of the true anal fin in Petromyzonidae, including *P. marinus*, is one of the most important

TABLE 4. Number of trunk myomeres and number of cusps on different teeth in three species of lampreys with two separate dorsal fins. Data refer to means and ranges (in parentheses) for each character. Data from sources mentioned in Table 2.

Species	*n*	Trunk myomeres	Supraoral cusps	Bicuspid endolaterals	Shape of lingual lamina	Posterials
P. marinus	131	70.1 (67–74)	2 (2)	4 (4) All bicuspid	Bilobed, strongly bent inward along median line and without enlarged median cusp	3–4 rows
L. lamottenii	89	68.9 (66–74)	2 (2)	3 (3) All bicuspid	Not bilobed, slightly convex on outer surface, median cusp enlarged	1 row
L. aepyptera	35	54.5 (50–59)	2 (2)	2 (1–3) Unicuspid, bicuspid, and tricuspid	Not bilobed, slightly convex on outer surface, median cusp enlarged	Absent

TABLE 5. Variation in the length of metamorphosed *Lethenteron lamottenii* from several localities. Data for Big Creek are from Kott (1974) and the remaining from Vladykov and Kott (1978).

No. of specimens	Total length (mm)		Locality
	Mean	Range	
13	110.2	102–125	Wednesday Brook, New Hampshire
8	130.1	125–140	Pont Rouge, Quebec
8	132.8	124–143	Furnace Creek, Lake Superior, Ontario
4	146.5	139–154	Sturgeon Bay, Wisconsin
10	152.4	145–165	Mad River, Ohio
6	166.9	160–173	Casadoga Creek, New York
10	167.3	158–177	Gatineau River, Quebec
20	173.3	145–192	Cranberry Creek, Lake Erie, Ontario
303	188.0	161–217	Big Creek, Lake Erie, Ontario

characteristics of the class Petromyzones. It was a most surprising find by the senior author (Vladykov 1973) of a female of *P. marinus* with a true anal fin. This lamprey, obtained in Big Creek, a tributary of Lake Erie, was 498 mm long and weighed 314 g. Its true anal fin, 31 mm in length, was supported by about 30 cartilagenous rays.

Recently Harold A. Purvis and Richard J. Schuldt (U.S. Fish and Wildlife Service, Marquette, Michigan) on June 6, 1979, collected in the Cheboygan River, tributary to Lake Huron, Cheboygan, Michigan, below the city dam, a female of *P. marinus*, 446 mm in length, weighing 251 g. It has an anal fin, inserted 21 mm behind the rear end of the anus. This fin is subdivided into two sections: a frontal lobe, 5 mm long at the base, and fin itself 28 mm in length at the base. The maximum height of the fin is 12 mm and that of the lobe 7 mm; the width of the lobe is 9 mm. In the middle of the fin proper, to the extent of 9 mm, about 36 fin rays are present. At the upper portion of the lobe, anteriorly and posteriorly, are also found 6 fin rays (Fig. 2). On the whole, in Cheboygan specimen, the anal fin rays were more numerous, but not as clearly visible as those in Vladykov's Big Creek female.

The cause of this most interesting abnormality in two females of *P. marinus* remains unknown to the authors.

Giant *Lethenteron lamottenii* in Great Lakes

The size of metamorphosed parasitic lampreys varies considerably, depending on their age and/or abundance of available food. Nonparasitic adult lampreys, deprived of a functional alimentary tract, do not feed and do not grow in length after their metamorphosis. For this reason variation in size of nonparasitic adult lampreys is rather limited (Vladykov and Kott 1979b).

An extensive variation in the length of adult *L. lamottenii* should be considered as an exception. Among 383 (Table 5) metamorphosed *L. lamottenii* from nine different localities, the variation in length was from 102 to 217 mm. The smallest specimens were obtained from Wednesday Brook, New Hampshire, and the largest one from Big Creek, Lake Erie, Ontario. However, Manion and Purvis (1971) described a capture of five nearly mature females, ranging in length from 260 to 299 mm (average 286 mm), weighing 37.2–46.0 g (average 41.1 g). They call these specimens "giant" American brook lampreys and described them as averaging "nearly twice as long and about six times as heavy as American brook lampreys of normal size." After a lapse of 16 yr, Richard J. Schuldt obtained, on May 2, 1977, a giant, nearly mature male of *L. lamottenii*, 317 mm in length (77.8 g) in the Peshtigo River, Lake Michigan, below the dam in Peshtigo, Wisconsin.

There are at least three possible explanations for the existence of giant *L. lamottenii* in the Great Lakes region.

1) Giant adults originate from giant ammocoetes of about 250–350 mm in length. These hypothetical ammocoetes could live in deep waters, hence are not seen by investigators. All nonparasitic adult lampreys with nonfunctional alimentary tracts reach their maximum size at completion of their metamorphosis. In other words, the size of nonparasitic adults is determined by the size of their ammocoetes.

2) Giant adults originate from adults of usual size, that is smaller than 200 mm. To reach their great length, they must continue to feed after metamorphosis, at least in the early period. This hypothesis is proposed by Manion and Purvis (1971), who assume that adult *L. lamottenii* may retain a functional alimentary tract for some time after completion of metamorphosis. Histological study by Battle and Hayashida (1965) does not confirm this. The second objection is based on *L. lamottenii* dentition. Although teeth of *L. lamottenii* are stronger than those of typical nonparasitic species such as *L. meridionale* or *L. alaskense*, they are not as sharp as in parasitic *L. japonicum*. The dentition of *L. lamottenii* can be compared with teeth of *Caspiomyzon wagneri*, which is a migratory species restricted to the Caspian Sea. Although its feeding habits are not yet fully understood (Vladykov and Kott

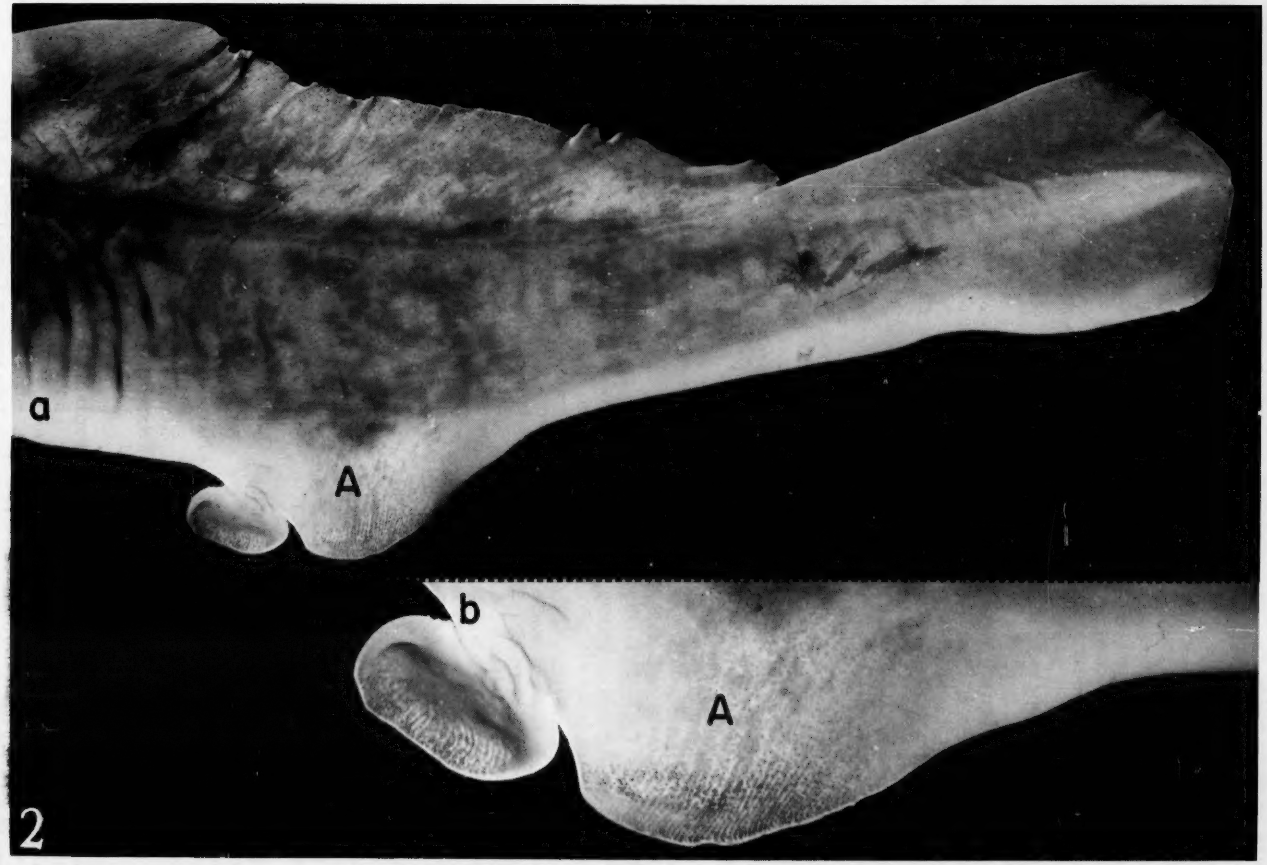

FIG. 2. Enlarged posterior section of *Petromyzon marinus* female from Cheboygan River, Michigan, with a true anal fin. (a) Position of subdivided anal fin (A) in relation to the caudal fin. (b) Magnified view of subdivided anal fin (A) with visible rays.

1979b), the size of this lamprey increases considerably after a sojourn of about 1 yr in the Caspian Sea. To judge by its blunt teeth, it cannot be parasitic on fish or other vertebrates. However, the possibility is not excluded that it feeds on demersal fish eggs or organic detritus. We can speculate that giant *L. lamottenii* feeds in the same fashion.

3) It is possible that the giant specimens of *L. lamottenii* represent a distinct race with different feeding requirements than typical nonparasitic *L. lamottenii*.

It is also puzzling that during nearly 20 yr only six specimens, five females and one male, were discovered. Why are giant individuals so rare? The question of the origin of even small numbers of giant specimens of the American brook lampreys is very important from both scientific and practical points of view. Therefore, we are planning to return to this problem in the near future.

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Applegate, V. C. 1950. Natural history of the sea lamprey, *Petromyzon marinus*, in Michigan. Spec. Sci. Rep. Fish. U.S. Dep. Int. Fish Wildlife Serv. 55: 1–237.

Bailey, R. M., J. E. Fitch, E. S. Herald, E. A. Lachner, C. C. Lindsey, C. R. Robins, and W. B. Scott. 1970. A list of common and scientific names of fishes from the United States and Canada. 3rd ed. Am. Fish. Soc. Spec. Publ. 6: 150 p.

Battle, H. I., and K. Hayashida. 1965. Comparative study of the intraperitoneal alimentary tract of parasitic and nonparasitic lampreys from the Great Lakes region. J. Fish. Res. Board Can. 22: 289–306.

Baxter, E. W. 1956. Observations on the buccal glands of lampreys (Petromyzontidae). Proc. Zool. Soc. Lond. 127: 95–118.

Beamish, F. W. H., and I. C. Potter. 1975. The biology of the anadromous sea lamprey (*Petromyzon marinus*) in New Brunswick. J. Zool. Lond. 177: 57–72.

Davis, R. M. 1967. Parasitism by newly transformed anadromous sea lampreys on landlocked salmon and other fishes in a coastal Maine lake. Trans. Am. Fish. Soc. 96: 11–16.

Distler, D. A. 1957. Some differential characteristics of ammocoetes of two species of lampreys, *Lampetra aepyptera* (Abbott) and *Lampetra lamottei* (LeSueur). M.Sc. thesis, Department of Biology, University of Louisville, KY.

Fowler, H. W. 1964. A catalog of world fishes. Vol. 1. Quart. Jr. Taiwan Mus. 17: 125–186.

Gibbs, S. P. 1956. The anatomy and development of the buccal glands of the lake lamprey (*Petromyzon marinus* Linnaeus) and the histochemistry of their secretion. J. Morphol. 98: 429–469.

Hagelin, L-O. 1959. Further aquarium observations on the spawning habits of the river lamprey (*Petromyzon fluviatilis*). Oikos 10: 50–64.

Hagelin, L-O, and N. Steffner. 1958. Notes on the spawning habits of the river lamprey (*Petromyzon fluviatilis*). Oikos 9: 221–238.

Hall, J. D. 1963. An ecological study of the chestnut lamprey, *Ichthyomyzon castaneus* Girard, the Manistee River, Michigan. Ph.D. thesis, Department of Zoology, University of Michigan, Ann Arbor, MI.

Hubbs, C. L., and K. Lagler. 1964. Fishes of the Great Lakes region. Univ. Mich. Press, Ann Arbor, MI. 213 p.

Hubbs, C. L., and M. B. Trautman. 1937. A revision of the lamprey genus *Ichthyomyzon*. Univ. Mich. Mus. Zool. Misc. Publ. 33: 109 p.

Kott, E. 1971. Characteristics of pre-spawning American brook lamprey from Big Creek, Ontario. Can. Field-Nat. 85: 235–240.

1974. A morphometric and meristic study of a population of the American brook lamprey, *Lethenteron lamottei* (LeSueur), from Ontario. Can. J. Zool. 52: 1047–1055.

Lawrie, A. H. 1970. The sea lamprey in the Great Lakes. Trans. Am. Fish. Soc. 99: 766–775.

Leach, W. J. 1940. Occurrence and life history of the northern brook lamprey, *Icthyomyzon fossor* in Indiana. Copeia 1940: 21–34.

Lelek, A. 1973. Occurrence of the sea lamprey in midwater off Europe. Copeia 1973: 136–137.

Manion, P. J. 1967. Morphological abnormalities among lampreys. Copeia 1967: 680–681.

Manion, P. J., and G. W. Piavis. 1977. Dentition throughout the life history of the landlocked sea lamprey *Petromyzon marinus*. Copeia 1977: 762–766.

Manion, P. J., and H. A. Purvis. 1971. Giant American brook lampreys, *Lampetra lamottei*, in the upper Great Lakes. J. Fish. Res. Board Can. 28: 616–620.

Manion, P. J., and B. R. Smith, 1978. Biology of larval and metamorphosing sea lampreys, *Petromyzon marinus*, of the 1960 year class in the Big Garlic River, Michigan, Part II, 1966–72. Great Lakes Fish. Comm. Tech. Rep. 20–35 p.

Moore, H. H., and R. A. Braem. 1965. Distribution of fishes in U.S. streams tributary to Lake Superior. U.S. Fish. Wildl. Spec. Sci. Rep. Fish. 516: 61 p.

Morman, R. H. 1979. Distribution and ecology of lampreys in the Lower Peninsula of Michigan, 1957–75. Great Lakes Fish. Comm. Tech. Rep. 33: 59 p.

Oliva, O. 1953. A contribution to the review of native lampreys (Petromyzones Berg 1940). Věstník Král. Čes. Spol. Nauk. Tř. Mat.-připrodověd 9: 1–19.

Piavis, G. W. 1961. Embryological stages in the sea lamprey and effect of temperature on development. U.S. Fish Wildlife Serv. Fish. Bull. 61: 111–143.

Potter, I. C., and F. W. H. Beamish. 1977. The freshwater biology of adult anadromous sea lampreys *Petromyzon marinus*. J. Zool. Lond. 181: 113–130.

Potter, I. C., and T. S. Osborne. 1975. The systematics of British larval lampreys. J. Zool. Lond. 176: 311–329.

Purvis, H. A. 1970. Growth, age at metamorphosis and sex ratio of northern brook lamprey in a tributary of southern Lake Superior. Copeia 1970: 326–333.

1979. Variations in growth, age at transformation, and sex ratio of sea lampreys re-established in chemically treated tributaries of the upper Great Lakes. Great Lakes Fish. Comm. Tech. Rep. 35: 36 p.

ROHDE, F. C., R. C. ARNDT, AND J. C. S. WANG. 1976. Life history of the freshwater lampreys *Okkelbergia aepyptera* and *Lampetra lamottenii* (Pisces: Petromyzonidae) on the Delmarva Peninsula (East Coast, United States). Bull. Southern Cal. Acad. Sci. 75: 99–110.

ROY, J.-M. 1973. Croissance, comportement et alimentation de la lamproie du nord (*Ichthyomyzon unicuspis*, Hubbs and Trautman) en captivité. Trav. Pêch. Que. 41: 144 p.

SEVERSMITH, H. F. 1953. Distribution, morphology and life history of *Lampetra* aepyptera, a brook lamprey, in Maryland. Copeia 1953: 225–232.

SMITH, B. R. 1971. Sea lampreys in the Great Lakes of North America, p. 207–247. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1, Academic Press, London.

TRAUTMAN, M. B. 1957. The fishes of Ohio. Ohio State University Press, Columbus, OH. 683 p.

VAN UTRECHT, W. L. 1959. Wounds and scars in the skin of the common porpoise, *Phocaena phocaena* (L.) Mammalia XXIII(I): 100–122.

VLADYKOV, V. D. 1949. Quebec lampreys (Petromyzonidae). 1. List of species and their economic importance. Contrib. Dep. Fish. Quebec 26: 67 p.

1950. Larvae of eastern American lampreys (Petromyzonidae). 1. Species with two dorsal fins. Nat. Can. 77: 73–95.

1960. Description of young ammocoetes belonging to two species of lampreys: *Petromyzon marinus* and *Entosphenus lamottenii*. J. Fish. Res. Board Can. 17: 267–288.

1972. Sous-division en trois sous-familles des lamproies de l'hémisphère-nord de la famille Petromyzonidae. ACFAS (Assoc. Can. Fr. Av. Sci.) 39: 148.

1973. A female sea lamprey (*Petromyzon marinus*) with a true anal fin, and the question of the presence of an anal fin in Petromyzonidae. Can. J. Zool. 51: 221–224.

VLADYKOV, V. D., AND W. I. FOLLETT. 1965. *Lampetra richardsoni*, a new nonparasitic species of lamprey (Petromyzonidae) from western North America. J. Fish. Res. Board Can. 22: 139–158.

1967. The teeth of lampreys (Petromyzonidae): their terminology and use in a key to the Holarctic genera. J. Fish. Res. Board Can. 24: 1067–1075.

VLADYKOV, V. D., AND E. KOTT. 1976. The taxonomic significance of velar tentacles in holarctic lampreys (Petromyzonidae). Rev. Trav. Inst. Pech. Marit. 40: 787–789.

1978. A new nonparasitic species of the holarctic lamprey genus *Lethenteron* Creaser and Hubbs, 1922, (Petromyzonidae) from northwestern North America with notes on other species of the same genus. Biol. Pap. Univ. Alaska 19: 74 p.

1979a. Satellite species among the holarctic lampreys (Petromyzonidae). Can. J. Zool. 57: 860–867.

1979b. List of Northern Hemisphere lampreys (Petromyzonidae) and their distribution. Fish. Mar. Serv. Misc. Spec. Pub. 42: 1–30.

VLADYKOV, V. D., E. KOTT, AND S. PHARAND-COAD. 1975. A new nonparasitic species of lamprey, genus *Lethenteron* (Petromyzonidae) from eastern tributaries of the Gulf of Mexico, U.S.A. Publ. Zool. 12. Natl. Mus. Can., Natl. Mus. Nat. Sci., Ottawa. Ont., 36 p.

VLADYKOV, V. D., AND G. N. MUKERJI. 1961. Order of succession of different types of infraoral lamina in landlocked sea lamprey (*Petromyzon marinus*). J. Fish. Res. Board Can. 18: 1125–1143.

VLADYKOV, V. D. ET J. M. ROY. 1948. Biologie de la lamproie d'eau douce (*Ichthyomyzon unicuspis*) après la métamorphose. Rev. Can. Biol. 7(3): 483–485.

YOUNG, J. Z. 1962. The life of vertebrates. 2nd ed. Oxford University Press, London.

Comments on the Classification and Nomenclature of Lampreys — An Alternative View[1]

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BAILEY, R. M. 1980. Comments on the classification and nomenclature of lampreys — an alternative view. Can. J. Fish. Aquat. Sci. 37: 1626–1629.

Current classifications of lampreys as reflected in this symposium are incongruent and unnecessarily split. It is suggested that modern lampreys be classified in one family, three subfamilies, and six genera. Most species are in a single genus *Lampetra* consisting of six subgenera. Intraspecific variation in dentition is greater than recognized previously. Reasons are given for use of the stem Petromyzont- for suprageneric names based on *Petromyzon*.

Key words: taxonomy, terminology, morphology, lampreys

BAILEY, R. M. 1980. Comments on the classification and nomenclature of lampreys — an alternative view. Can. J. Fish. Aquat. Sci. 37: 1626–1629.

Les classifications actuelles des lamproies, telles que reflétées par le présent colloque, sont un clivage à la fois incongru et superflu. Les lamproies modernes devraient être classées en une famille, trois sous-familles et six genres. La plupart des espèces sont dans un genre unique, *Lampetra*, comprenant six sous-genres. La variation intraspécifique de la dentition est plus grande que celle reconnue dans le passé. Nous donnons les raisons pour lesquelles le préfixe Petromyzont-, fondé sur *Petromyzon*, devrait être employé pour les noms supragénériques.

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THE two foremost active students of the systematics of lampreys are participants in this symposium. Individually and with collaborators, I. C. Potter and V. D. Vladykov have been prolific contributors to knowledge of lampreys, their systematics, morphology, life histories, ecology, evolution, and diverse aspects of biology. Yet, when their classifications and nomenclatural recommendations are juxtaposed, the reader is understandably confused by incongruities. He or she must wonder which, if either, advocates an acceptable arrangement. Although not a specialist on lampreys, I am relatively conversant with the systematics and literature of the group, have handled most of the species as a museum curator, and, as a member of the Names Committee of the American Fisheries Society, represent a nomenclatural constituency different from the authors of either of the preceding papers. In preparation of the fourth edition of ***A List of Common and Scientific Names of Fishes from the United States and Canada***, that committee has attempted to evaluate the numerous contributions to lamprey systematics of the past decade, many of which derive from the researches of Drs Potter and Vladykov and their collaborators. Based in part on that assessment, my own conclusions on lamprey classification and nomenclature are incorporated in this commentary.

Higher Group Nomenclature

Names of higher groups (subfamily to order) based on *Petromyzon* have long been in a state of flux. The family name Petromyzonidae was used by Hubbs and Potter (1971) and by Vladykov and coauthors (many papers); Petromyzontidae was preferred by Bailey et al. on AFS lists in 1960 and 1970 (which use has been followed by many workers and some journals, including the Canadian Journal of Fisheries and Aquatic Sciences and its predecessor, the Journal of the Fisheries Research Board of Canada). Petromyzontidae is of long standing, having been used through most of the late 19th century by, among others, Agassiz (1850), Günther (1870), Gage (1893), and T. Gill (1893). Gill (1895: 110), however, contended that the conventional orthography was erroneous, "was due to a false analogy," and revived Bonaparte's spelling Petromyzonidae. He has been widely followed. I have discussed this problem with Howard D. Cameron, classicist and arthropod systematist at The University of Michigan, who tells me that it is evident from his comment that Gill simply did not know enough Greek to realize that his argument is nonsense. It is Gill who has created the false analogy. Dr. Cameron assures me that the name is a compound of the present participle of myzō (to suck) and the appropriate stem (the genitive singular without its case ending) is petro-

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[1] This paper forms part of the Proceedings of the Sea Lamprey International Symposium (SLIS) convened at Northern Michigan University, Marquette, Michigan, July 30–August 8, 1979.

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TABLE 1. Equivalence of classifications of the genera and subgenera (in parentheses) allied to *Lampetra* (tribe Lampetrini) by some recent authors.

Bailey (this paper)	Hubbs and Potter (1971)	Potter (1980)	Vladykov and Kott (1979)
Lampetra (*Entosphenus*)	*Lampetra* (*Entosphenus*)	*Lampetra* (*Entosphenus*)	*Entosphenus*
Lampetra (*Tetrapleurodon*)	*Tetrapleurodon*	*Tetrapleurodon*	*Tetrapleurodon*
Lampetra (*Lethenteron*)	*Lampetra* (*Lethenteron*)	*Lampetra* (*Lethenteron*)	*Lethenteron*
Lampetra (*Eudontomyzon*)	*Eudontomyzon*	*Eudontomyzon*	*Eudontomyzon*
Lampetra (*Lampetra*)	*Lampetra* (*Lampetra*)	*Lampetra* (*Lampetra*, in part)	*Lampetra* (in part)
Lampetra (*Okkelbergia*)	*Okkelbergia*	*Lampetra* (*Lampetra*, in part)	*Lampetra* (in part)

myzont-; hence, Petromyzontidae is grammatically correct. This same conclusion was reached independently by Steyskal (1980: 173).

A request for a ruling on the spelling of the family name has been addressed to the International Commission on Zoological Nomenclature by V. D. Vladykov and C. G. Gruchy. When the issue is decided most persons will probably abide by the judgment whether or not they agree. Meanwhile it seems appropriate to continue prevailing practice in use of Petromyzontidae, as was done by Hubbs, Follett, and Dempster (1979: 1, 3). Two of these authors had earlier been coauthors with Potter and Vladykov in publications that used Petromyzonidae. The stem Petromyzont- would be used also for ordinal (suffix-iformes), superfamily (-oidea), subfamily (-inae), and tribe (-ini) names if these categories are used.

Lamprey Families and Subfamilies

Traditionally all modern lampreys have been grouped in a single family, occasionally in two or three families. Potter and Strahan (1968: 234–236) discussed the family status at some length. They considered that the known genera fall into three groups, but felt that the degree of difference was worthy only of subfamilial distinction. They recognized three subfamilies, one including the Northern Hemisphere lampreys (Petromyzoninae) and two (Geotriinae, with a single species and Mordaciinae, with three species) for the Southern Hemisphere forms. Without material change in understanding of relationships, Hubbs and Potter (1971: 32–36) elevated each of these to family level. Dealing only with the Holarctic species, which they ranked as a family, Vladykov and Kott (1979: 860) classified that group in three subfamilies (Petromyzoninae, Lampetrinae, and Entospheninae), and eight genera.

Classifications of Recent fishes suffer from a superfluity of families; 450 in one moderately conservative recent work, 554 in another that is more finely split. Significantly, each of these treats the lampreys as a single family. Recent lampreys make up a small group of about three dozen species. No one, to my knowledge, challenges the integrity of Recent lampreys as a monophyletic assemblage. Communication is facilitated by recognition of one instead of three groups at one of the major levels in the classificatory hierarchy — the family. The three principal groups of living lampreys may be conveniently designated as subfamilies, as by Potter and Strahan (1968). The primary dichotomy in the Holarctic lampreys (Petromyzontinae) may be used to separate two tribes, Petromyzontini (*Ichthyomyzon*, *Petromyzon*, and *Caspiomyzon*) and Lampetrini (*Lampetra*).

Genera and Subgenera

This discussion concerns only the Holarctic lampreys here assigned to the single genus *Lampetra* (tribe Lampetrini); there is current agreement on genera of the Southern Hemisphere lampreys and those of the Petromyzontini. Uniquely in *Lampetra*, the supraoral lamina is a broad, transverse, or crescent-shaped plate with an enlarged cusp at either end; one or more smaller intermediate cusps may or may not be developed. The configuration of the supraoral plate is interpreted as a derived character state. The cohesive monophylety of this group is here emphasized by treatment at the generic level. The distinctiveness of included inferior groups is indicated by subgeneric partition.

The unevenness assigned to groups of lampreys in classification is glaringly emphasized by the ranking of *Lampetra* (sensu stricto) and *Entosphenus*: as subgenera of *Lampetra* by Hubbs and Potter (1971) and Potter (1980); in subfamilies Lampetrinae and Entospheninae by Vladykov and Kott (1979). Hubbs and Potter recognized *Lampetra* (s.s.), *Entosphenus*, and *Lethenteron* as subgenera of *Lampetra* (sensu lato); all were accorded generic status by Vladykov and Kott. On the other hand, Hubbs and Potter (1971: 36) provisionally adopted a genus *Okkelbergia* for the single species *aepyptera*; this species was included in *Lampetra* (s.s.) by Vladykov and Kott (1976), an action accepted by Potter in the present volume. Otherwise the nomenclature of Potter's (1980) paper closely follows that of Hubbs and Potter (1971). Equivalent schemes of classification are summarized in Table 1.

The diversity in classification noted above and illustrated in Table 1 results from at least three factors: disagreement in the relative evaluation of character differences, different interpretation of phyletic relationships among the species and groups, and philosophical outlook toward splitting and lumping.

Recognition of the genera *Tetrapleurodon* (Mexico) and *Eudontomyzon* (Eurasia) and their phyletic association by Hubbs and Potter (1971: 37, 39) depended largely on their common possession of numerous villiform, sharply pointed teeth on the anterior, lateral, and sometimes even posterior fields of the oral disc. *Okkelbergia*, despite its excessively degenerate dentition, also has a few minute teeth in these fields. Valuable as these may be as aids to identification, however, teeth in these areas characterize also all species of Southern Hemisphere lampreys and the Petromyzontini. Their presence may thus be shared primitive states and may not provide reliable evidence of close relationship. In contrast, *Entosphenus* and *Tetrapleurodon* were associated by Vladykov and Follett (1967: 1073), and later by Vladykov and Kott (1979: 860) as the "Entospheninae." These groups characteristically share four lateral circumorals (or inner laterals), probably a primitive feature, similarity of the transverse lingual lamina, and the usual or common occurrence of a median cusp in the supraoral plate, at least in parasitic species, likely shared derived features. Both of these groups are of North Pacific distribution; *Entosphenus* species are anadromous or freshwater, *Tetrapleurodon* is confined to the Lerma River basin of Mexico. *Tetrapleurodon* would appear to be an isolated southern geographic relict derived from a formerly more widely ranging anadromous common ancestor. The geographic distribution of *Eudontomyzon* and *Tetrapleurodon* offers no such suggestive evidence of common origin. *Entosphenus* and *Tetrapleurodon* are so similar morphologically and appear to be so intimately related that even their subgeneric separation is questionable.

Hubbs and Potter overemphasized the importance of inner disc teeth in *Lampetra*, but Vladykov and Kott assigned undue significance to the posterior closure of the circumoral ring, i.e. their "posterials." This tooth series is characteristically complete and well defined in the Petromyzontini, in *Entosphenus*, *Tetrapleurodon*, and *Eudontomyzon*; it is invariably absent in *Lampetra* (s.s.). Variable development of this series in *Lethenteron* and *Okkelbergia* reduces its utility and clearly militates against its use in the separation of genera. Most species of *Lethenteron* have a well-formed, continuous series of posterior circumorals. But an Italian species was described as *Lampetra zanandreai* by Vladykov (1955), who reported that "mandibular labials" were lacking. As previously reported by Hubbs and Potter (1971: 53), however, Zanandrea (1958) has shown that in *zanandreai* the series of posterior circumorals is variable, being present in 74 of 180 individuals. The series was well developed and complete in most of these; a few had the ring broken into three arcs, one central and two lateral and symmetrical; another had three or four little teeth on each side. The typical cusp formula of lateral circumorals was 2–2–2 (reported by Vladykov as 2–3–2), the usual formula in *Lethenteron*, whereas the species of *Lampetra* (s.s.) most often have 2–3–2. Hubbs and Potter (1971: 53) therefore assigned *zanandreai* to *Lethenteron*, ranked by them as a subgenus, a placement unacceptable to Vladykov and Kott (1979: 864). Zanandrea detected the posterior circumorals in this nonparasitic lamprey by use of a vital stain in narcotized specimens.

Lampetra (*Okkelbergia*) *aepyptera*, a small nonparasitic species from eastern United States, presents potentially confusing variations. Reduction in its dentition is extreme among lampreys. The teeth are few, small, poorly cornified, and many are often invisible in macroscopic examination of alcoholic specimens. They are readily visible, however, in alizarin-stained preparations. In a study underway by Ted M. Cavender of Ohio State University and myself, we discover that, as in *L. zanandreai*, the posterior–circumoral tooth series may be wholly wanting, represented by one or a few irregularly disposed teeth, partly developed, or complete. Scattered additional teeth may be present in all fields of the disc. The marginal teeth are more irregularly disposed than in other species of *Lampetra* and often form two or more rows. The dentition confirms the uncertain systematic position of *aepyptera* (Hubbs and Potter 1971: 39, 48–49), but this clearly does not warrant exclusion from *Lampetra* (s.l.). Vladykov and Kott (1976) assigned *aepyptera* to *Lampetra* (s.s.), but they did this without knowledge of dental variation. *Lethenteron meridionale* (Vladykov, Kott, and Pharand-Coad 1975), based on specimens with an evident series of posterior circumoral teeth, is a synonym of *Lampetra aepyptera*. Thus, like *L. zanandreai*, *L. aepyptera* bridges the gap between *Lampetra* (s.s.) and *Lethenteron* as defined by Vladykov and his collaborators. Its distinctive features, alluded to above and including the reduced number of velar tentacles (3), may warrant retention of the subgenus *Okkelbergia* for its sole reception, at least until new insight into its relationships is forthcoming.

Several authors have accepted *Lampetra* with relatively broad limits (i.e. including *Eudontomyzon*, *Tetrapleurodon*, and/or *Lethenteron*) with the exception that *Entosphenus* was assigned separate generic status (e.g. Berg 1931; Bailey et al. 1970; McPhail and Lindsey 1970), for the reception of the single species *tridentatus*. During the past decade five purportedly new species of *Entosphenus*, two parasitic and three nonparasitic, have been described. Several of the former character discontinuities between *Entosphenus* and other groups of the Lampetrini have disappeared and justification for generic ranking is accordingly diminished. For example, salient characters of *L. tridentata* such as the strong median cusp of the supraoral plate, the numerous (11–16) velar tentacles, and high myomere count (62–74) must be expanded to include absence of the median cusp, as few as three velar tentacles, and a low myomere count of 53.

In summary of the above paragraphs on genera, I believe that Vladykov and Kott's classification more accurately describes the close relationship of *Tetrapleurodon* and *Entosphenus* than does that of Hubbs and Potter (1971) or Potter (1980). The generic nomenclature of these authors is inferior to that of Berg (1931). I would modify that only by reduction of *Entosphenus* from generic to subgeneric rank in *Lampetra*. The arrangement of Vladykov and Kott is a splitter's classification; they do not use the rank of subgenus and upgrade other groups unnecessarily. *Okkelbergia* may for the present be recognized as a subgenus of *Lampetra*, probably the most degenerate (or specialized) of lampreys. Interrelationships among the six suggested subgenera of *Lampetra* are not well understood.

Species

Many species of lampreys have been proposed as new in recent years. It seems clear that some of these are valid. I have remarked above that *Lethenteron meridionale* is a synonym of *Lampetra aepyptera*. The nominal *Lethenteron alaskense* Vladykov and Kott seems to differ from the eastern American brook lamprey (see below) chiefly in distribution. The ultimate disposition of some additional nominal species awaits future research, but a few of these are probably untenable. One potentially rewarding avenue of research concerns explanation of phenotypic reduction in myomere number in several southern species or populations. If these are shown to be ecophenotypes, some species based chiefly on myomere count may need to be synonymized.

The American brook lamprey was formerly known as *Lampetra* (or *Entosphenus*) *appendix*. In recent years it has been generally called *L. lamottei* or *L. lamottenii*. R. M. Bailey and F. C. Rohde (MS) will recommend the suppression of *Petromyzon lamottenii* Lesueur as unidentifiable, and adopt the name *Lampetra appendix* (DeKay), an action anticipated in the 4th edition of the list of names of fishes (Robins et al. 1980).

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AGASSIZ, L. 1850. On the Petromyzontidae and their embryonic development and place in the natural history system. Edinburgh New Philos. J. 49: 242–246.

BAILEY, R. M., J. E. FITCH, E. S. HERALD, E. A. LACHNER, C. C. LINDSEY, C. R. ROBINS, AND W. B. SCOTT. 1970. A list of common and scientific names of fishes from the United States and Canada (3rd ed.). Am. Fish. Soc. Spec. Publ. 6: 1–149.

BAILEY, R. M., E. A. LACHNER, C. C. LINDSEY, C. R. ROBINS, P. M. ROEDEL, W. B. SCOTT, AND L. P. WOODS. 1960. A list of common and scientific names of fishes from the United States and Canada (2nd ed.). Am. Fish. Soc. Spec. Publ. 2: 1–102.

BERG, L. S. 1931. A review of the lampreys of the northern hemisphere. Ann. Mus. Zool. Acad. URSS 32: 87–116.

GAGE, S. H. 1893. The lake and brook lampreys of New York. Wilder Quarter-Century Book. p. 421–493.

GILL, T. 1893. Families and subfamilies of fishes. Mem. Nat. Acad. Sci. 6: 127–138.

1895. On the nomenclature and characteristics of lampreys. Proc. U.S. Nat. Mus. 17(989): 107–110.

GÜNTHER, A. 1870. Catalogue of the fishes in the British Museum. Vol. 8. London. 549 p.

HUBBS, C. L., W. I. FOLLETT, AND L. J. DEMPSTER. 1979. List of the fishes of California. Occ. Pap. Calif. Acad. Sci. 133: 1–51.

HUBBS, C. L., AND I. C. POTTER. 1971. Distribution, phylogeny and taxonomy, p. 1–65. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. I. Academic Press, New York.

MCPHAIL, J. D., AND C. C. LINDSEY. 1970. Freshwater fishes of northwestern Canada and Alaska. Bull. Fish. Res. Board Can. 173: 1–381.

POTTER, I. C. 1980. The Petromyzoniformes with particular reference to paired species. Can. J. Fish. Aquat. Sci. 37: 1595–1615.

POTTER, I. C., AND R. STRAHAN. 1968. The taxonomy of the lampreys *Geotria* and *Mordacia* and their distribution in Australia. Proc. Linn. Soc. Lond. 179(2): 229–240.

ROBINS, C. R., R. M. BAILEY, C. E. BOND, J. R. BROOKER, E. A. LACHNER, R. N. LEE, AND W. B. SCOTT. 1980. A list of common and scientific names of fishes from the United States and Canada. 4th ed. Am. Fish. Soc. Spec. Publ. 12. (In press)

STEYSKAL, G. C. 1980. The grammar of family-group names as exemplified by those of fishes. Proc. Biol. Soc. Wash. 93: 168–177.

VLADYKOV, V. D. 1955. *Lampetra zanandreai*, a new species of lamprey from northern Italy. Copeia (3): 215–223.

VLADYKOV, V. D., AND W. I. FOLLETT. 1967. The teeth of lampreys (Petromyzonidae): their terminology and use in a key to the holarctic genera. J. Fish. Res. Board Can. 24: 1067–1075.

VLADYKOV, V. D., AND E. KOTT. 1976. Is *Okkelbergia* Creaser and Hubbs, 1922 (Petromyzonidae) a distinct taxon? Can. J. Zool. 54: 421–425.

1979. Satellite species among the holarctic lampreys (Petromyzonidae). Can. J. Zool. 57: 860–867.

VLADYKOV, V. D., E. KOTT, AND S. PHARAND-COAD. 1975. A new nonparasitic species of lamprey, genus *Lethenteron* (Petromyzonidae), from eastern tributaries of the Gulf of Mexico, U.S.A. Nat. Mus. Nat. Sci. (Ottawa) Publ. Zool. 12: 1–36.

ZANANDREA, G. 1958. Posizione sistematica e distribuzione geografica di Lampetra Zanandreai Vladykov. Mem. Mus. Civ. Stor. Nat. Verona 6: 207–237.

Detection of Variability at Isozyme Loci in Sea Lamprey, *Petromyzon marinus*[1,2]

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KRUEGER, C. C. 1980. Detection of variability at isozyme loci in sea lamprey, *Petromyzon marinus*. Can. J. Fish. Aquat. Sci. 37: 1630–1634.

Electrophoretic expression of 20 enzymes coded by a minimum of 30 gene loci is reported for sea lamprey. ADA, ADH, AGP, AAT, CPK, G6PDH, GAPDH, LDH, MDH, PEP, 6PGD, PGI, PGK, PGM, PK, PMI, and SDH yielded gel resolution satisfactory for use in future population studies. Six loci, *AGP*, *MDH-1*, *PGI-1*, *PGI-2*, *PGM-1*, and *PMI* were polymorphic. Enzyme expression did not vary between life stages (ammocoete vs. adult) or collection method (fresh frozen vs. TFM killed). Statistically significant genetic differences occurred between lamprey from Lake Superior, Oneida Lake, Lake Champlain, and Bay of Fundy drainages at one or more of the polymorphic loci.

Key words: isozyme, lamprey, *Petromyzon*, electrophoresis, population identification, polymorphism

KRUEGER, C. C. 1980. Detection of variability at isozyme loci in sea lamprey, *Petromyzon marinus*. Can. J. Fish. Aquat. Sci. 37: 1630–1634.

Le présent article décrit l'expression électrophorétique de 20 enzymes codés à l'aide d'au moins 30 loci géniques chez la grande lamproie marine. ADA, ADH, AGP, AAT, CPK, G6PDH, GAPDH, LDH, MDH, PEP, 6PDG, PGI, PGK, PGM, PK, PMI et SDH donnent sur gel une résolution suffisante pour usage dans de futures études de population. Six loci, *AGP*, *MDH-1*, *PGI-1*, *PGI-2*, *PGM-1* et *PMI*, sont polymorphes. L'expression enzymique ne varie pas d'un stade à l'autre du cycle biologique (ammocète vs adulte) ou selon la méthode de collection (congelé frais vs tué au TFM). Il existe des différences génétiques significatives à l'analyse statistique entre les grandes lamproies marines des lacs Supérieur, Oneida, Champlain et des bassins hydrographiques de la baie de Fundy à un ou plusieurs des loci polymorphes.

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THE sea lamprey, *Petromyzon marinus*, is a marine species which gained access to the upper Great Lakes of North America following the construction of the Welland Canal in 1829. Predation by the lamprey has subsequently led to the collapse of commercially valuable stocks of lake trout, *Salvelinus namaycush*, in Lakes Huron and Michigan, and caused precipitous declines in abundance of lake trout and whitefish, *Coregonus clupeaformis*, in Lake Superior (Smith 1968; Lawrie and Rahrer 1972; Christie 1974). The damage caused by the sea lamprey fostered an intensive control program, organized between the United States and Canadian governments and directed by the Great Lakes Fishery Commission (Smith 1971; Smith et al. 1974; Crowe 1975).

Although the present control program relies to a large extent upon a chemical toxicant directed toward larval lampreys in the tributary streams, it is now believed to be important to develop alternative control methods and integrated management programs (Smith and Tibbles 1980; Hanson and Manion 1980). The successful construction and implementation of any management program frequently requires information with regard to the genetic organization of the populations of concern (Smith et al. 1976; Allendorf and Utter 1979). Identification of lamprey populations would provide the fundamental unit upon which to structure management strategies.

The focus of the present research was to describe electrophoretically the products of enzyme loci that will be useful in later intensive studies concerning the genetic identification of lamprey populations in the Great Lakes. The utility of the loci for lamprey population identification is demonstrated through an analysis of four geographically discrete populations.

Earlier, electrophoretic studies with this fish have been concerned with questions of a taxonomic or physiological nature (e.g. Wilson et al. 1964; Thomas and McCrimmon 1964; Uthe et al. 1966; Uthe and

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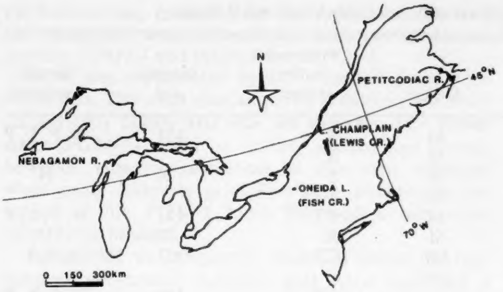

FIG. 1. Sea lamprey ammocoete collection locations.

Tsuyuki 1967; Horowitz and Whitt 1972; Whitt et al. 1975). Population discrimination by electrophoresis has not previously been attempted for this species.

Materials and Methods

Sea lamprey ammocoetes were collected by electrofishing from four localities: Nebagamon River, Lake Superior drainage; Fish Creek, Oneida Lake drainage; Lewis Creek, Lake Champlain drainage; and Petitcodiac River, Bay of Fundy drainage (Fig. 1). Animals from Nebagamon R. were transported alive and held in aquaria at the University of Minnesota for ~1 mo before analysis. The other specimens were frozen as soon as possible after collection and stored at −20°C. Ammocoetes from the Nebagamon River were used in the initial screening for the enzymatic activity. Enzymes that exhibited sufficient activity on the gels were then electrophoretically examined among lamprey from all locations.

Electrophoretic expressions of enzymes were also compared between fresh-frozen and TFM (3-trifluoromethyl-4-nitrophenol)-killed lampreys. Fourteen ammocoetes from Nebagamon River were held in an aquarium and exposed to 12 mg/L TFM. Death occurred in ~4 h. A single individual, also used in the analysis, was killed by a 1-h exposure to 40 mg/L TFM. Fresh-frozen ammocoetes from the same river were used as controls in the gels. Chemical analysis of the well water used in the aquaria for these experiments has been given by Adelman and Smith (1972).

Electrophoretic enzyme patterns were also compared between ammocoetes (40–100 mm), newly transformed adults (110–145 mm), and spawning adults (375–445 mm). Ammocoetes were from the Nebagamon River while the newly transformed adults were from the St. John's River, New Brunswick. Spawning adults used in the analysis were captured from the Brule River, Wisconsin.

Lampreys were prepared for electrophoresis by the removal of viscera and skin. Usually, muscle located caudally from the gill pouches was used as a tissue sample. When ammocoetes were less than 45 mm in length, the entire animal was used. Muscle tissue samples were prepared for electrophoresis in a similar manner to that described by Krueger and Menzel (1979).

Gels, 20.5 × 15.2 × 0.9 cm, were prepared with 58.8 g of hydrolyzed potato starch (Electrostarch Co., Madison, WI) in 420 mL of gel buffer. Electrophoretic techniques followed those detailed by May et al. (1979). Four different buffer systems were used:

A) Ridgway et al. (1970). Gel: 0.03 mol/L Tris–0.005 mol/L citric acid, pH 8.5; Electrode: 0.06 mol/L lithium hydroxide–0.3 mol/L boric acid, pH 8.1. Gels were made with 99% buffer and 1% electrode buffer. Potential: 200V for 5 h.

B) Clayton and Tretiak (1972). Gel: 0.002 mol/L citric acid, pH 6.0. Electrode: 0.04 mol/L citric acid, pH 6.1. Both buffers were pH-adjusted with *N*-(3-Aminopropyl)-morpholine. Potential: 185V for 5 h.

C) Selander et al. (1971). Gel: 1:9 dilution of electrode buffer. Electrode: 0.10 mol/L Tris–0.10 mol/L maleic acid–0.1 mol/L EDTA(ethylenediamene-tetraacetic acid)–0.01 mol/L magnesium chloride, pH 7.4. Potential: 100V for 5 h.

D) Whitt (1970). Stock solution: 0.75 mol/L Tris–0.25 mol/L citric acid, pH 6.9: Gel: 1:60 dilution of stock. Electrode: 1:20 dilution of stock. Potential: 200V for 5 h.

Staining procedures generally followed those given by Allendorf et al. (1977). An exception was aspartate aminotransferase (glutamate oxalate transaminase) staining which followed Selander et al. (1971). Another recipe alteration was phosphomannose isomerase (PMI) staining which used 100 mg of Ba-D-mannose-6-phosphate. The substrate for the peptidase stain was glycyl-L-leucine. Genic nomenclature used here is that proposed by Allendorf and Utter (1979) for salmonids (see also May et al. 1979). Tests for statistical homogeneity between sets of phenotypic frequencies at the polymorphic loci utilized chi-square in contingency tables (Snedecor and Cochran 1967:250).

Results and Discussion

ELECTROPHORETIC EXPRESSION OF ENZYMES

Among 25 enzymes studied, 20 exhibited sufficient activity to designate loci (Table 1). Banding patterns observed from these 20 enzymes represent the products of a minimum of 30 gene loci. The number of loci coding for a particular enzyme was estimated conservatively. For example, single invariant bands were treated as if they were expressions from one gene locus. Such bands may represent the products of a number of loci that share a common allele for a particular enzyme. The exact number of loci, therefore, cannot be determined.

Enzymes yielding gel resolution satisfactory for use in future population studies are ADA, ADH, AGP, AAT, CPK, G6PDH, GAPDH, LDH, MDH, PEP, 6PGD, PGI, PGK, PGM, PK, PMI, and SDH. Although zones of activity occurred for AK, ALD, and FDP, banding patterns were either faint or poorly defined and therefore are not recommended for population surveys using present methods. Little or no staining activity occurred on the gels for diaphorase, glutamate dehydrogenase, hexokinase, succinate dehydrogenase, and xanthine dehydrogenase.

The enzymes suitable for population surveys are coded by a minimum of 26 loci (Table 1). Among these loci, six were polymorphic within the four populations studied: *AGP*, *MDH-1*, *PGI-1*, *PGI-2*, *PGM-1*, and *PMI*.

TABLE 1. Results of screening for electrophoretically detectable loci in sea lamprey.

Enzyme	Locus	Alleles[a]	Preferred buffer system[b]	Sample size	Sample location[c]
Adenosine deaminase	*ADA-1*	M	S	131	N, F, L, P
	ADA-2	M	S		
Adenylate kinase	*AK-1*	M	S	20	N
	AK-2	M	S		
Alcohol dehydrogenase	*ADH*	M	CT	131	N, F, L, P
Aldolase	*ALD*	M	R	20	N
Alpha-glycerophosphate dehydrogenase	*AGP*	*100*	CT	107	N, F, L
		146			
Aspartate aminotransferase	*AAT-1*	M	CT	152	N, F, L, P
	AAT-2	M	CT		
Creatine phosphokinase	*CPK-1*	M	S	20	N
	CPK-2	M	S		
Diaphorase[d]	—	—	—	20	N
Fructose-1,6-diphosphatase	*FDP*	M	S	141	N, F, L, P
Glutamate dehydrogenase[d]	—	—	—	20	N
Glucose-6-phosphate dehydrogenase	*G6PDH*	M	W or S	120	N, F, L, P
Glyceraldehyde-3-phosphate dehydrogenase	*GAPDH-1*	M	W or CT	30	N
	GAPDH-2	M	W or CT		
Hexokinase[d]	—	—	—	20	N
Lactate dehydrogenase	*LDH*	M	R	152	N, F, L, P
Malate dehydrogenase	*MDH-1*	*−100*	CT	152	N, F, L, P
		−165			
	MDH-2	M	CT		
	MDH-3	M	CT		
Peptidase	*PEP-1*	M	S	132	N, F, L, P
	PEP-2	M	S		
6-Phosphogluconate dehydrogenase	*6PGD*	M	S	141	N, F, L, P
Phosphoglucose isomerase	*PGI-1*	*100*	R	160	N, F, L, P
		130			
	PGI-2	*100*	R		
		122			
		92			
Phosphoglycerate kinase	*PGK*	M	W	20	N
Phosphoglucomutase	*PGM-1*	*100*	R	132	N, F, L, P
		148			
	PGM-2[e]	—	—		
Pyruvate kinase	*PK*	M	W or S	131	N, F, L, P
Phosphomannose isomerase	*PMI*	*100*	CT	20	N
		90			
Sorbitol dehydrogenase	*SDH*	M	R	151	N, F, L, P
Succinate dehydrogenase[d]	—	—	—	30	N
Xanthine dehydrogenase[d]	—	—	—	20	N

[a] M = monomorphic.

[b] R = Ridgway et al. (1970); CT = Clayton and Tretiak (1972); S = Selander et al. (1971); W = Whitt (1970).

[c] N = Nebagamon River; F = Fish Creek; L = Lewis Creek; P = Petitcodiac River.

[d] Insufficient staining activity to designate loci.

[e] Enzyme activity present but gels were not scorable.

AGP migrated anodally and exhibited three phenotypes. The genetic control of the variability observed for this dimeric enzyme was ascribed to a single locus with two alleles.

Enzyme products of *MDH-1* (supernatant) migrated cathodally and exhibited polymorphism. The phenotypes for this dimeric enzyme fit a two-allele model with heterozygotes represented by a three-banded pattern. The *MDH-1* (*-165*/*-165*) phenotype was not observed. Two invariant MDH bands, possibly mitochondrial forms, migrated anodally and are tentatively proposed to be the products of two loci, *MDH-2* and *MDH-3*. Heterodimeric products between the three loci were not observed on the gels.

PGI activity in sea lamprey was typically expressed as a three-banded phenotype on the gels. The two outer bands represent homodimeric products from separate loci, *PGI-1* and *PGI-2*. The middle band is the heterodimer formed from the products of the two loci. Both loci were polymorphic with two alleles occurring at *PGI-1* and three alleles at *PGI-2*.

PGM was represented by two zones of activity on Whitt gels. The most anodal zone (tentatively *PGM-2*) stained only faintly and was not scorable. The slower zone (*PGM-1*) could be reliably stained and scored; however, superior resolution of this zone occurred when using Ridgway gels. The three phenotypes observed at the *PGM-1* locus followed a two allele monomeric model.

When PMI was originally examined within the four lamprey collections, Selander gels were used and a strong monomorphic single band was observed for all individuals. Later it was discovered that by increasing the staining substrate, polymorphic banding patterns could be observed on Clayton–Tretiak gels. Twenty fish from the Nebagamon River have so far been analyzed in this manner. Three phenotypes were observed for this monomeric enzyme and their genetic control was ascribable to a single-locus, two-allele model.

ADH, G6PDH, LDH, 6PGD, PGK, PK, and SDH were all represented as a single invariant band on the gels; each of these enzymes was designated as if coded by one locus (Table 1).

ADA, AAT, GAPDH, and PEP all exhibited two isozymes of different electrophoretic mobility. No variation in banding patterns was observed for this group. Two loci were assumed responsible for the genetic control of each of these enzymes.

The dimeric enzyme CPK in sea lamprey was represented by a single cathodal band and two anodal bands. The zone between the origin and the first anodal band appeared to be faintly stained by AK. Thus far, no variation has been observed in CPK. Two loci were assumed to control the electrophorectic patterns.

Ammocoete sea lamprey enzyme expressions were also compared between animals killed by exposure to TFM and those killed by freezing. Gels were stained for ADA, ADH, AGP, AAT, FDP, G6PDH, LDH, MDH, PEP, 6PGD, PGI, PGM, PMI, PK, and SDH. In every case, no differences were observed in enzymatic expression between lamprey subjected to different modes of euthanasia. TFM does not appear to alter these enzymes in an electrophoretically detectable way. Ammocoetes, newly transformed adults, and spawning adults were also compared for the same enzymes listed above. Similarly no difference in enzymatic expression was observed. Uthe and Tsuyuki (1967) found that the transformation process in sea lamprey electrophoretically affected blood proteins but not general muscle proteins.

GENETIC VARIABILITY OBSERVED BETWEEN LOCALITIES

Variability in the expressions of *AGP*, *MDH-1*, *PGI-1*, *PGI-2*, and *PGM-1* were analyzed in sea lamprey from four localities (Table 2). *AGP* was highly variable in allelic frequencies between Nebagamon River, Fish Creek, and Lewis Creek. Gels with tissue samples from the Petitcodiac River stained for AGP were not scorable because of a lack of enzymatic activity. *MDH-1* allelic frequencies were fixed for the common allele in ammocoetes from Fish Creek and Lewis Creek but variable in collections from Nebagamon River and Petitcodiac River. At the *PGI-1* locus, variability was only observed in ammocoetes from the Petitcodiac River. At the *PGI-2* locus, the Nebagamon River had a unique alternate allele (*92*) not observed in the other three collections. Fish Creek specimens were the most variable at *PGI-2* of the four collections. *PGM-1* variability was greatest for lamprey from Nebagamon River while the other collection locations had similar allelic balances. Phenotypic frequencies observed for these six loci in lamprey were all in conformity with Hardy–Weinberg expectations.

TABLE 2. Allelic frequencies for five polymorphic loci in sea lamprey. Sample sizes (*n*) are included.

Locus		Nebagamon River	Fish Creek	Lewis Creek	Petitcodiac River
AGP	*100*	0.67	0.42	0.84	NA
	146	0.33	0.58	0.16	NA
	n	41	31	35	NA
MDH-1	*−100*	0.86	1.00	1.00	0.81
	−165	0.14	0.0	0.0	0.19
	n	62	31	30	29
PGI-1	*100*	1.00	1.00	1.00	0.97
	130	0.0	0.0	0.0	0.03
	n	70	31	30	29
PGI-2	*100*	0.98	0.76	0.93	0.93
	92	0.02	0.0	0.0	0.0
	122	0.0	0.24	0.07	0.07
	n	70	31	30	29
PGM-1	*100*	0.77	0.97	0.97	0.95
	148	0.23	0.03	0.03	0.05
	n	42	31	30	29

Paired comparisons of phenotypic frequencies by locus were made between collections using χ^2. Statistically significant differences ($P < 0.05$) were demonstrated between collection localities at one or more loci. Genetic distances (Rogers 1972) between samples, however, were small suggesting little interpopulation genetic divergence (Table 3).

The results of this study demonstrate the capabilities

TABLE 3. Genetic distance (Rogers 1972) between sea lamprey collections. Data at *AGP* were excluded from distance calculations.

Collection location	Nebagamon River	Fish Creek	Lewis Creek
Fish Creek	0.030	—	—
Lewis Creek	0.021	0.009	—
Petitcodiac River	0.017	0.002	0.013

of electrophoretic techniques in population identification of sea lampreys. The presence of unique alleles in lamprey from Nebagamon River (*PGI-2 92*) and in the Petitcodiac River (*PGI-1 130*) may provide the means to study zoogeographical patterns of sea lamprey with respect to origins of invasion to the upper Great Lakes. In addition, sufficient variability was displayed at the polymorphic loci, particularly *AGP*, *MDH-1*, *PGM-1*, and *PMI*, to allow the study of allelic composition of sea lamprey populations within the Great Lakes.

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Adelman, I. R., and L. L. Smith Jr. 1972. Toxicity of hydrogen sulfide to goldfish (*Carassius auratus*) as influenced by temperature, oxygen, and bioassay techniques. J. Fish. Res. Board Can. 29: 1309–1317.

Allendorf, F. W., N. Mitchell, N. Ryman, and G. Stahl. 1977. Isozyme loci in brown trout (*Salmo trutta* L.): detection and interpretation from population data. Hereditas 86: 179–190.

Allendorf, F. W., and F. W. Utter. 1979. Population genetics, p. 407–454. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology, Vol. VIII. Academic Press, NY.

Christie, W. J. 1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Board Can. 31: 827–854.

Clayton, J. W., and D. N. Tretiak. 1972. Amine–citrate buffers for pH control in starch gel electrophoresis. J. Fish. Res. Board Can. 29: 1169–1172.

Crowe, W. R. 1975. Great Lakes Fishery Commission history, program, and progress. Great Lakes Fish. Comm., Ann Arbor, MI. 21 p.

Hanson, L. H., and P. J. Manion. 1980. Sterility method of pest control and its potential role in an integrated sea lamprey (*Petromyzon marinus*) control program. Can. J. Fish. Aquat. Sci. 37: 2108–2117.

Horowitz, J. J., and G. S. Whitt. 1972. Evolution of a nervous system specific lactate dehydrogenase isozyme in fish. J. Exp. Zool. 180: 13–32.

Krueger, C. C., and B. W. Menzel. 1979. Effects of stocking on genetics of wild brook trout populations. Trans. Am. Fish. Soc. 108: 277–287.

Lawrie, A. H., and J. F. Rahrer. 1972. Lake Superior: effects of exploitation and introductions on the salmonid community. J. Fish. Res. Board Can. 29: 765–776.

May, B., J. E. Wright, and M. Stoneking. 1979. Joint segregation of biochemical loci in Salmonidae: results from experiments with *Salvelinus* and review of the literature on other species. J. Fish. Res. Board Can. 36: 1114–1128.

Ridgway, F. J., S. W. Sherburn, and R. D. Lewis. 1970. Polymorphism in the esterases of Atlantic herring. Trans. Am. Fish. Soc. 99: 146–151.

Rogers, J. S. 1972. Measure of genetic similarity and genetic distance. Studies in Genetics VII. Univ. Tex. Publ. 7213: 145–153.

Selander, R. K., M. H. Smith, S. Y. Yang, W. E. Johnson, and J. B. Gentry. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old field mouse (*Peromyscus polionotus*). Studies in Genetics VI. Univ. Tex. Publ. 7103: 49–90.

Smith, B. R. 1971. Sea lampreys in the Great Lakes of North America, p. 207–247. *In* M. W. Hardisty and I. C. Potter [ed.] The Biology of lampreys. Vol. 1. Academic Press, NY.

Smith, B. R., and J. J. Tibbles. 1980. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936–78. Can. J. Fish. Aquat. Sci. 37: 1780–1801.

Smith, B. R., J. J. Tibbles, and B. G. H. Johnson. 1974. Control of the sea lamprey (*Petromyzon marinus*) in Lake Superior, 1953–70. Great Lakes Fish. Comm. Tech. Rep. 25: 60 p.

Smith, M. H., H. O. Hillestad, M. N. Manlove, and R. L. Marchinton. 1976. Use of population genetics data for the management of fish and wildlife populations. Trans. 41 North Am. Wildl. Nat. Res. Conf. p. 119–133.

Smith, S. H. 1968. Species succession and fishery exploitation in the Great Lakes. J. Fish. Res. Board Can. 25: 667–693.

Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods. Iowa State Univ. Press, Ames, IA. 593 p.

Thomas, M. L. H., and H. R. McCrimmon. 1964. Variability in paper electrophoretic patterns of the serum of landlocked sea lamprey *Petromyzon marinus* Linnaeus. J. Fish. Res. Board Can. 21: 239–246.

Uthe, J. F., E. Roberts, L. W. Clarke, and H. Tsuyuki. 1966. Comparative electropherograms of representatives of the families Petromyzontidae, Esocidae, Centrarchidae, and Percidae. J. Fish. Res. Board Can. 23: 1663–1671.

Uthe, J. F., and H. Tsuyuki. 1967. Comparative zone electropherograms of muscle myogens and blood proteins of adult and ammocoete lamprey. J. Fish. Res. Board Can. 24: 1269–1273.

Whitt, G. S. 1970. Developmental genetics of the lactate dehydrogenase isozymes of Fish. J. Exp. Zool. 175: 1–36.

Whitt, G. S., J. B. Shaklee, and C. L. Markert. 1975. Evolution of the lactate dehydrogenase isozymes of fishes, p. 381–400. *In* C. L. Markert [ed.] Isozymes IV, genetics and evolution. Academic Press, NY.

Wilson, A. C., N. O. Kaplan, L. Levine, A. Pesce, M. Reishlin, and W. S. Allison. 1964. Evolution of lactic dehydrogenase. Fed. Proc. 23: 1258–1266.

Spawning Behavior and Fecundity of Lampreys from the Upper Three Great Lakes[1]

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Five species of lampreys are found in the upper three Great Lakes. All species require certain physical factors for successful spawning such as suitable bottom substrates, water velocities, and temperatures. Nest construction (usually started by males) and spawning behavior are similar although some differences exist. In sea lamprey an average spawning act lasts about 2–5 s and is repeated every 4–5 min; generally nesting is monogamous with little polyandrous nesting (1.2–5.0%); average egg production is about 60 000 eggs. An estimated 86% of the eggs of sea lamprey are not deposited in the nests; however, the fertilization and survival of eggs deposited in the nest is high and may approach 90%.

Key words: Petromyzon marinus, Ichthyomyzon unicuspis, I. castaneus, I. fossor, Lampetra lamottei, spawning requirement, nest construction, fecundity, nest productivity, water temperature

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On trouve cinq espèces de lamproies dans la partie supérieure des Grands Lacs. Chez toutes, le succès de la ponte dépend de certains facteurs physiques tels que substrat convenable, vitesse du courant et température de l'eau. La nidification (ordinairement commencée par les mâles) et le comportement reproducteur sont semblables, bien qu'il existe quelques différences. Chez la grande lamproie marine, l'acte reproducteur dure en moyenne approximativement 2–5 s et se répète à intervalles de 4 à 5 min; l'occupation du nid est généralement monogamme, avec très peu polyandrie (1,2–5,0%); la production moyenne d'oeufs est environ 60 000. On estime que 86% des oeufs de la grande lamproie marine ne sont pas déposés dans les nids; cependant, la fécondation et la survie des oeufs déposés dans les nids est élevée, pouvant atteindre 90%.

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BAILEY et al. (1970) lists 14 species of lampreys in the United States and Canada. Five species are found in tributaries to lakes Superior, Michigan, and Huron and include three parasitic species: sea lamprey, *Petromyzon marinus*; silver lamprey, *Ichthyomyzon unicuspis*; chestnut lamprey, *Ichthyomyzon castaneus*; and two nonparasitic species: American brook lamprey, *Lampetra lamottei* and northern brook lamprey, *Ichthyomyzon fossor*. The landlocked sea lamprey in the Great Lakes has been studied in more detail than any of the other species. Electrical barriers were operated in the Great Lakes from 1953 to 1979 — first to control sea lampreys by preventing upstream migration of adults (McLain et al. 1965) and then later for assessment. The operation of the electrical barriers, along with observations on spawning lampreys by personnel in the sea lamprey control program over a 26-yr period, provided much of the data used in this study.

This paper describes the spawning behavior, nest construction, larval production, and fecundity of sea lampreys and presents some information on other species in the upper three Great Lakes.

Spawning Requirements

SEA LAMPREY

Certain physical factors are essential for successful sea lamprey spawning (Applegate 1950). One requirement is a steady, unidirectional flow of water. Lampreys observed attempting to construct nests in waters that change direction or velocity become confused and often leave the nest. McLain et al. (1965) considered chang-

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ing water flows as the reason successful spawning has not taken place along the lakeshores in the Great Lakes. Also needed are suitable substrates of sand and gravel (about 0.9–5.1 cm in diameter), along with satisfactory water velocities (0.5–1.5 m/s), depths ranging from 13 to 170 cm, and temperatures ranging from 10.0 to 26.1°C. Sea lampreys prefer the upstream edge of a graveled riffle or the riffle area proper for nesting sites.

Sea lampreys start to migrate in early spring (April), and some are found in the river as late as September 15, the latest recorded date (McLain et al. 1965). Sea lampreys usually do not start to build nests until the water warms to about 15°C, which generally occurs in June in the upper Great Lakes. Often sudden drops of 1 or 2°C during the early part of the spawning season are followed by a cessation or slowing of nesting (Applegate 1950; Manion and McLain 1971). Generally major spawning takes place in June–July.

OTHER SPECIES

The physical factors needed by sea lampreys to spawn successfully also are required by the other four lamprey species in the upper Great Lakes. Preferred gravel substrates differ according to size of the lamprey. For example, silver lampreys (average length, 250 mm) use intermediate-sized gravel (0.4–3 cm in diameter) while American brook lampreys (average length, 150 mm) often nest in gravel about pea size. Smaller lampreys also prefer lower water velocities and shallower water depths. Hardisty and Potter (1971) describe typical brook lamprey streams as having water velocities of about 0.3–0.5 m/s in spawning areas.

Spawning seasons of the five species overlap, although the total length of the season is longer for the sea lamprey (May–September) than for the other four species (April–July). American brook lampreys spawn the earliest and initiate spawning in the coldest water, about 7°C (Rohde et al. 1976; Morman 1979). The other three species generally spawn at average water temperatures of about 18°C (Morman 1979).

Nest Construction and Spawning Behavior

SEA LAMPREY

Sea lampreys enter a stream several weeks before spawning and are not observed even under intense searching during daylight hours (Manion and McLain 1971). Once nesting starts, lampreys apparently become tolerant to light and migrate and spawn in bright sunlight. The eyes of sea lampreys often become opaque as the spawning season progresses; perhaps they lose their aversion to light because their vision becomes less acute.

Nest construction among sea lampreys is usually started by males, although Applegate (1950) noted that females also initiated nest construction toward the end of the spawning season when they were numerically dominant. The male sea lamprey constructs a small depression about 20 cm in diameter in the gravel which it occupies until joined by a female. Males rarely elaborate on the nest after construction of the initial depression until joined by females.

Active nest construction begins after the female joins the male and construction is accompanied by frequent spawning acts. Sea lampreys move a rock downstream by attaching to it with the oral sucker, twisting back and forth until the rock is dislodged, and dragging it downstream with the aid of the current. Lampreys of both sexes sometimes join together to remove a particularly large rock, but it appears to be an accidental occurrence. The lampreys deposit rocks to form a crescent-shaped mound on the downstream side, although they occasionally deposit rocks upstream or to the side of the nest. The behavior of lampreys in moving rocks stirs up sand on the stream bottom and exposes more rocks which also are removed by the lampreys, creating a deep depression.

Nest construction normally takes 1–3 d. The dimensions of a typical sea lamprey nest are about 45 cm wide (perpendicular to the stream flow) and 40 cm long, with a downstream crest 8 cm high. "Community" nests — nests constructed side by side so close together that individual nests lose their identity — are sometimes observed completely spanning a stream (Manion and McLain 1971).

There appears to be another variation of behavior in the vibratory body action of sea lampreys during nest building independent of the moving of rocks and spawning action. Lampreys often attach to a rock and with vigorous whipping movements fan the nest, thereby creating a cloud of sand which drifts to the rear of the nest. They apparently perform this action to cover the eggs and protect them from predation. We also observed eggs being released by ripe females during the fanning action.

The general spawning act for sea lampreys has been previously described (Gage 1928; Applegate 1950). Descriptions by other investigators indicate the spawning act, with minor variations, is similar for different species. The female, with her head facing upstream, attaches with her oral disc to a large stone usually located at the upstream margin of the nest. The male approaches the female near the second dorsal fin, glides with his mouth along her body toward the head, and fastens himself firmly to the top of the head, usually over the nasopore region. If the female is not firmly attached to the stone or releases her attachment (even though the male may be attached), the spawning act is not completed. Once the male fastens to the head of the female, he curves the posterior one-third of his body around the female so that their genital pores are in close proximity. Fertilization is not internal in lampreys in the upper Great Lakes and the genital papilla serves only to direct the sperm and not as a copulatory organ. The female actively vibrates her body within the circular fold of the male and together by contracting their bodies they expel eggs and sperm simultaneously. The fertilized eggs are nonbuoyant and adhesive and are carried by the current to the rear of the nest where they lodge in the gravel and sand just upstream to the crest. At the end of each mating act, the male releases his hold on the head of the female and both resume construction of the nest. An average spawning act lasts about 2–5 s and is repeated about every 4–5 min among actively spawning pairs. Spawning adults flushed from a nest usually return shortly and resume nesting and spawning. The number of eggs extruded during each spawning act has not been positively determined for any species in the Great Lakes, although Applegate (1950) estimated that sea lamprey extrude between 20 and 40 eggs.

Generally, sea lampreys are monogamous spawners, although observations by various investigators show the proportion of monogamy varies. Applegate (1950) observed 84% monogamous nesting in the Ocqueoc River, a tributary to Lake Huron. Two studies conducted on the Big Garlic River, a tributary to Lake Superior, in 1974 and 1976 (Hanson and Manion 1978, 1980) show that the incidence of monogamy was 56% in 1974 and 87% in 1976. They suggested that sex ratios determine the number of females in each nest and the lower incidence of monogamous nesting in 1974 was possibly due to the higher proportion of females in the spawning population. The percentage of female lampreys released in the Big Garlic River was 50 in 1974, compared with 19 in 1976.

Applegate (1950) and Manion and McLain (1971) found polyandrous nesting to be relatively rare among sea lampreys — usually from 1 to 5%. Hanson and Manion (1978, 1980) found no polyandrous nesting in their studies even though in one study (1980), the ratio of males to females was 300:70. Nesting was considered to be polyandrous if more than one male in a nest spawned with the same female and the males were not antagonistic toward each other.

Male sea lampreys establish and protect a nesting territory and are often observed fighting for nests. The antagonism between males also appears to increase once the male is joined by a female. During an attack the resident male flares its mouth, attaches to the head or branchial region of the invader, and viciously removes it from the nest area. The victorious male then returns to the nest and resumes nest construction and spawning. Females show no preference for specific males.

Most investigators agree that all lamprey species spawn only once in their life and lampreys that have no opportunity to spawn die also. The extreme degeneration of the internal organs and the external appearance of the animals during and after spawning leaves no doubt that they die shortly after spawning.

OTHER SPECIES

Nests of the four other species of lampreys are not as visible and are less well defined than those of the sea lamprey. Silver lampreys (intermediate-sized) build nests about 30 cm in diameter with a cavity depth of 11 cm, while nests of brook lampreys often are only small, oval-shaped depressions about 18 cm in diameter and 8 cm deep (Morman 1979).

Other lamprey species sometimes spawn in nests previously constructed by sea lampreys, and spawning lampreys of different species often share a common nest — usually a sea lamprey nest (Morman 1979). The nest associations appeared compatible, and there was no indication of antagonistic behavior between species.

Some lampreys engage in mass spawning. Case (1970) noted up to 50 chestnut lampreys in one nest, and Morman (1979) stated that for northern brook lampreys there was an average of about seven per nest. The males in these nests do not have the competitive characteristic of sea lamprey, although competitiveness has been noted among American brook lampreys (Young and Cole 1900; Gage 1928).

Fecundity and Production of Larvae

SEA LAMPREY

The fecundity of sea lampreys has been determined by various investigators (Table 1). Average egg production estimates ranged from 55 913 for Lake Huron to 68 599 for Lake Superior. Fecundity of the anadromous sea lamprey far exceeds that of the landlocked form and fecundities of the former ranged from 151 836 to 304 832 eggs with a mean of 210 228 eggs (Beamish and Potter 1975). Fecundity is related to the length of the adult in that the number of eggs increases with increased length, although the numbers of eggs vary greatly at any particular length. For example, mean estimated egg production of four lampreys 376 mm long ranged from 43 997 to 72 329 eggs (Manion 1972). Fecundity estimates in relation to length or weight also may be strongly affected by the time of collection. Manion and McLain (1971) found that a progressive loss in length and weight of adults was directly correlated with the number of days the adults were in the river. Because of this loss of length and weight, lampreys collected early in the spawning season undoubtedly have fewer eggs per unit of length or weight than those captured later.

Although fecundity of sea lampreys is high, few eggs survive to hatching under natural conditions. Hatching success has been estimated for the sea lamprey by Manion (1968), who removed all embryos from 19 nests in two Lake Superior streams. The hatching success from these nests based on fecundity estimates of Applegate (1950) averaged 6.3% (range, 5.3–7.8%). Since Applegate (1950) determined the proportion of larvae emerging from three single nests in the Ocqueoc River, a tributary of Lake Huron, to be only 0.4, 0.7, and 1.1%, possibly some larvae in the nests he ex-

TABLE 1. Estimates of fecundity, mean lengths, and mean water temperatures during spawning for lampreys from the upper three Great Lakes. (Ranges in parentheses.)

Species and estimated number of eggs	Mean length (mm)	Mean water temp. (°C)	Reference
Ichthyomyzon castaneus			
—	216 (105–310)	—	Hubbs and Trautman (1937)
—	—	16.5	Case (1970)
—	207 (178–250)	18.3 (15.6–22.2)	Morman (1979)
I. fossor			
—	—	22.0	Reighard and Cummins (1916)
—	119 (94–146)	—	Hubbs and Trautman (1937)
1200 (1050–1340)	—	—	Leach (1940)
1524 (1115–1979)	138 (128–150)	—	Vladykov (1951)
—	114 (97–129)	—	Purvis (1970)
—	115 (86–166)	18.0 (12.8–23.3)	Morman (1979)
I. unicuspis			
—	—	22.2	Greeley (1930)
—	224 (103–328)	—	Hubbs and Trautman (1937)
19 012 (12 006–29 412)	255 (201–305)	—	Vladykov (1951)
—	246 (201–305)	—	Marion and Purvis (1971)
—	248 (157–308)	18.3 (12.8–22.8)	Morman (1979)
Lampetra lamottei			
—	—	17.2	Young and Cole (1900)
3276	156 (143–170)	(10.0–12.8)	Gage (1893, 1928)
2339 (1085–3648)	143 (116–158)	17.0	Vladykov (1951)
—	132 (110–169)	(10.0–11.0)	Hardisty (1961)
—	154 (111–196)	—	Manion and Purvis (1971)
—	179 (159–205)	—	Kott (1971)
1691 (1327–2070)	124 (119–132)	(6.8–12.0)	Rohde et al. (1976)
—	—	14.1 (6.7–20.6)	Morman (1979)
Petromyzon marinus			
61 500 (21 000–107 138)	442 (320–536)	15.5	Applegate (1950) Lake Huron
62 870 (38 678–85 712)	359 (291–439)	—	Vladykov (1951) Lake Michigan
55 913 (28 891–74 023)	384 (330–435)	—	Lake Huron
—	—	14.0 (12.8–18.3)	Manion and McLain (1971)
68 599 (43 997–101 932)	462 (340–511)	—	Manion (1972) Lake Superior
—	—	15.7 (10.0–22.8)	Hanson and Manion (1978)
—	—	18.2 (11.1–26.1)	Morman (1979)

amined were buried in such a way that they were not able to leave the nest.

Some factors which lower total nest productivity are unspawned eggs, water temperatures, and deposition or retention of eggs in the nest. Applegate (1950) found that between 0 and 37% (mean 5%) of ripe eggs remained in 40 spent females (Lake Huron). All females with a high percentage of residual eggs had spawned near the end of the spawning season. Manion and McLain (1971) determined that unspawned eggs for 28 females from Lake Superior averaged 2.2% (range, 0.3–6.7%) as estimated from the length of females at the time of release and that longer females retained relatively more eggs than shorter ones. Hanson and Manion (1978) determined that an average of 1.2% of the eggs remained in 10 spent females.

Water temperatures undoubtedly are critical in the production of viable larvae, but apparently the fluctuating temperatures that occur in nature can extend the subsequent temperature tolerance of the developing embryos. Piavis (1961) described the effects of different constant temperatures on the embryological development of the sea lamprey. He stated that burrowing larvae were produced only from eggs incubated at temperatures from 15.6 to 21.1°C (optimum 18.3°C). He advised, however, that although his findings offered strong evidence that unsuitable temperatures may have accounted for the failure of some streams to produce larval sea lampreys, a too close application of the results to conditions found in nature was not recommended. Under natural conditions, water temperatures in streams fluctuate widely and embryos are often subjected to far lower temperatures than those expressed as lethal (15.6°C) by Piavis (1961). During the spawning season and period of embryological development in the Big Garlic River in 1960 (June 27 to about August 4), eggs were subjected to water temperatures that fluctuated between 10.0 and 18.3°C (Manion and McLain 1971). For 28 of the 39 d, the mean daily temperatures were below the postulated lethal level of 15.6°C. Later determinations of the larval population showed that survival was high. During a study on the same river in 1974 (Hanson and Manion 1978), the first pair of lampreys was observed spawning on June 26 when water temperatures ranged from 10.0 to 11.7°C. Small samples of eggs were removed from this nest 12, 18, and 28 d after deposition. Embryonic development was slower in the lower water temperatures. Embryos took 12, 18, and 28 d to reach stages 10, 14, and 16[2]; stages that Piavis (1961) described as taking 10, 13, and 17 d, respectively, at 18.3°C. Although development was slow, the survival rate of the embryos ranged from 85 to 97% for the three samples. It is apparent that for varying periods of time developing embryos can withstand temperatures previously considered to be lethal.

Perhaps the major reason for low larval production is that of the large numbers of eggs extruded many are not deposited or retained in the nest during spawning. Many eggs drift over the crest of the nest during the spawning act and are swept downstream by the current upon release. Other eggs are swept from the nest by water currents during nest construction as lampreys continue to work on nests, dislodging stones and stirring up sand and predeposited eggs. Sometimes another pair of lampreys will spawn in an existing nest and totally rearrange the position of the nest. All of these activities result in the loss of eggs from the nest. Although the fate of these eggs is unknown, they are subjected to the water turbulence of gravel areas and because of stream hydrology may be deposited in silt or sand where they probably suffer high mortalities. Predation by fish in and below lamprey nests also has been observed (Manion 1968).

To determine the proportion of eggs retained in nests, Hanson and Manion (1980) removed all eggs from 74 sea lamprey nests constructed in the Big Garlic River by an introduced population of 70 females and 300 males. A total of 745 375 eggs were counted in these nests. Actual egg counts in each nest ranged from 103 to 34 310 and averaged 10 073. Nests located behind rocks or submerged logs generally had larger numbers of eggs. Apparently these obstructions slowed or changed the direction of the current over the nest so that eggs were more readily deposited in the nest. On the basis of estimates of fecundity and numbers of residual eggs (Applegate 1950), the 70 females (average length, 489 mm) produced about 5 530 000 eggs of which 276 500 eggs (5%) were retained by the females, leaving an estimated total of 5 253 500 eggs available for spawning. Since only 745 375 were collected from the nests prior to emergence, it follows that 4 508 125 eggs (86%) were spawned but not deposited or retained in the nests.

Although the percentage of eggs deposited in nests is small, the survival of eggs so deposited appears to be high. Survival could only be determined in 3 of the 74 nests in our study because many eggs had been fertilized by sterile males (Hanson and Manion 1980). However, in one nest 22 162 of 23 456 (94%) of the embryos were in stages 13 and 14, and in two other nests the survival of deposited eggs to stages 13 and 14 was 85%. In four nests sampled in the Big Garlic River in 1977, the survival rate of deposited eggs to stages 13–16 averaged 88% (Hanson and Manion 1978). Thus, fertilization and survival of eggs deposited in the nests were quite high and probably averaged about 90% in nests where normal males spawned.

OTHER SPECIES

Fecundity of the sea lampreys far exceeds that of the other four species in the Great Lakes. Average fecundities for *I. fossor* and *L. lamottei* and *I. unicuspis* with mean lengths of 115, 154, and 247 mm were 1524, 2339, and 19 012 eggs, respectively (Table 1). Although fecundities have not been determined for *I. castaneus*, their length (average 216 mm) would indicate fecundities slightly below those of *I. unicuspis*.

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[2] Among the stages of development (Piavis 1961), stages 1–13 describe the development of the embryos from zygote to hatching (stage 14), and stages 15 (pigmentation) and 16 (gill-cleft formation) describe the development of the prolarvae until they are able to leave the nest and burrow in the bottom mud (stage 17).

The factors that limit total nest productivity of sea lampreys probably also apply to the other four lamprey species, although no data is available on hatching success, deposition or retention of eggs in nests, survival or temperature tolerance.

Implications of Information on Spawning Behavior and Fecundity in Lamprey Control

Basic research on the biology of sea lampreys is essential for successful control of this pest in the Great Lakes. Research studies fill a void or add to the existing knowledge necessary in developing and interpreting various control measures.

Studies on the spawning requirements of sea lampreys indicate that certain modifications of spawning habitat may exert a high degree of control on natural populations. It has been suggested by S. H. Smith (1303 Ironwood St., Boulder City, NV, personal communication) that such measures as the reforestation of certain streams may reduce water temperature below that necessary for successful lamprey reproduction.

A thorough knowledge of the normal nest building and spawning behavior of sea lampreys is essential for evaluating lamprey chemosterilants. Only those methods of sterilization which do not affect mating competitiveness will be useful in a sterile-male-release program. Information on fecundity and larvae production will be useful in establishing synthesis models. Models are becoming increasingly useful in assessing the role that larvicides, chemosterilants, attractants, and other forms of control play in an integrated control program.

Applegate, V. C. 1950. Natural history of the sea lamprey *Petromyzon marinus* in Michigan. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. 55: 237 p.

Bailey, R. M., J. E. Fitch, E. S. Herald, E. A. Lachner, C. C. Lindsey, C. R. Robins, and W. B. Scott. 1970. A list of common and scientific names of fishes from the United States and Canada. Am. Fish. Soc. Spec. Publ. 6: 150 p.

Beamish, F. W. H., and I. C. Potter. 1975. The biology of the anadromous sea lamprey *Petromyzon marinus* in New Brunswick. J. Zool. London 177: 52–72.

Case, B. 1970. Spawning behavior of the chestnut lamprey *Ichthyomyzon castaneus*. J. Fish. Res. Board Can. 27: 1872–1874.

Gage, S. H. 1893. The lake and brook lampreys of New York, especially those of Cayuga and Seneca Lakes, p. 421–493. *In* Wilder Quarter-Century Book, Ithaca.

1928. The lampreys of New York State — life history and economics. *In* Biological survey of the Oswego River system. New York Conserv. Dept. Suppl. 17th Ann. Rep. 1927: 158–191.

Greeley, J. R. 1930. Fishes of the Lake Champlain watershed. Rep. N.Y. State Conserv. Dep. 19 (Suppl.): 44–87.

Hanson, L. H., and P. J. Manion. 1978. Chemosterilization of the sea lamprey, *Petromyzon marinus*. Great Lakes Fish. Comm. Tech. Rep. 16: 35 p.

1980. Sterility method of pest control and its potential role in an integrated sea lamprey (*Petromyzon marinus*) control program. Can. J. Fish. Aquat. Sci. 37: 2108–2117.

Hardisty, M. W. 1961. Studies on an isolated spawning population of brook lampreys *Lampetra planeri*. J. Anim. Ecol. 30: 339–355.

Hardisty, M. W., and I. C. Potter. 1971. The general biology of adult lampreys, p. 127–206. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, Inc., London.

Hubbs, C. L., and M. B. Trautman. 1937. A revision of the lamprey genus *Ichthyomyzon*. Museum Zool. Univ. Michigan Press Misc. Publ. 35: 109 p.

Kott, E. 1971. Characteristics of prespawning American brook lampreys from Big Creek, Ontario. Can. Field-Nat. 85(3): 235–240.

Leach, W. J. 1940. Occurrence and life history of the northern brook lamprey *Ichthyomyzon fossor* in Indiana. Copeia 1940: 21–34.

Manion, P. J. 1968. Production of sea lamprey larvae from nests in two Lake Superior streams. Trans. Am. Fish. Soc. 97: 484–486.

1972. Fecundity of the sea lamprey *Petromyzon marinus* in Lake Superior. Trans. Am. Fish. Soc. 101: 718–720.

Manion, P. J., and A. L. McLain. 1971. Biology of larval sea lampreys *Petromyzon marinus* of the 1960 year class, isolated in the Big Garlic River, Mich. 1960–65. Great Lakes Fish. Comm. Tech. Rep. 16: 35 p.

Manion, P. J., and H. A. Purvis. 1971. Giant American brook lampreys *Lampetra lamottei* in the upper Great Lakes. J. Fish. Res. Board Can. 28: 616–620.

McLain, A., B. R. Smith, and H. H. Moore. 1965. Experimental control of sea lampreys with electricity on the south shore of Lake Superior, 1953–60. Great Lakes Fish. Comm. Tech. Rep. 10: 48 p.

Morman, R. H. 1979. Distribution and ecology of lampreys in the Lower Peninsula of Michigan. Great Lakes Fish. Comm. Tech. Rep. 33: 59 p.

Piavis, G. W. 1961. Embryological stages in the sea lamprey and effects of temperature on development. U.S. Fish. Wildl. Serv. Fish. Bull. 61: 111–143.

Purvis, H. A. 1970. Growth, age at metamorphosis, and sex ratio of northern brook lamprey in a tributary of southern Lake Superior. Copeia 1970: 326–332.

Reighard, J., and H. Cummins. 1916. Description of a new species of lamprey of the genus *Ichthyomyzon*. Occ. Pap. Mus. Zool. Univ. Michigan 31: 1–12.

Rohde, F. C., E. G. Arnat, and J. C. S. Wang. 1976. Life history of the freshwater lampreys *Okkelbergia aepyptera* and *Lampetra lamottenii*. Bull. Soc. California Acad. Sci. 75(2): 99–111.

Vladykov, V. D. 1951. Fecundity of Quebec lampreys. Can. Fish. Cult. 10: 14 p.

Young, R. T., and L. J. Cole. 1900. On the nesting habits of the brook lamprey *Lampetra wilderi*. Am. Nat. 34: 617–620.

Ecology of Larval and Metamorphosing Lampreys[1]

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POTTER, I. C. 1980. Ecology of larval and metamorphosing lampreys. Can. J. Fish. Aquat. Sci. 37: 1641–1657.

Ammocoetes are relatively sedentary burrowing animals. Movement is related to water discharge, temperature, and season, and occurs predominantly downstream and at night. Growth is asymptotic and seasonal. At the end of larval life, the ammocoete ceases to increase markedly in length and starts to accumulate lipid. Length–frequency curves and data on kidney growth indicate that, in relatively stable and productive sites, ammocoetes of long established populations of the landlocked and anadromous sea lamprey take ~ 5 yr to reach metamorphosing length. Many animals probably enter transformation within a further 3 yr. Information from an isolated population in the Big Garlic River and from other tributaries of lakes Superior and Michigan, some of which had been treated with larvicide, shows that the onset of metamorphosis can be highly variable and is apparently related to the growth rates and size of larvae. A short larval life is usually associated with a fast growth rate of ammocoetes, as is sometimes found in rivers where the use of larvicide has reduced population density. The landlocked sea lamprey tends to metamorphose at a longer length and at a greater age than other parasitic lampreys. During metamorphosis, which usually begins in the summer, lampreys maintain length but lose weight as a result of mobilization of lipid. The time between initiation of transformation and onset of feeding is generally 4–10 mo. The downstream migration of metamorphosed animals is nocturnal and is influenced by freshwater discharge. Comparisons are drawn between the sex ratios of sea lampreys in the upper Great Lakes and those of other populations.

Key words: ammocoete, habitats, growth, mortality, larvicide, lipid, metamorphosis, migration, sex ratio, Great Lakes

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Les ammocètes sont des animaux fouisseurs relativement sédentaires. Leurs mouvements sont affectés par le débit d'eau, la température et la saison, et se produisent surtout vers l'aval et la nuit. La croissance est asymptotique et saisonnière. À la fin de leur phase larvaire, les ammocètes cessent presque complètement de croître et commencent à accumuler des lipides. Les courbes de fréquence de longueur et les données sur la croissance du rein indiquent que, à des endroits relativement stables et productifs, les ammocètes de populations établies de longue date de grandes lamproies marines cantonnées en eau douce et anadromes prennent environ 5 ans pour atteindre la longueur de métamorphose. Pour plusieurs sujets, la métamorphose sera retardée d'une période allant jusqu'à 3 ans. Des observations faites sur une population isolée de la rivière Big Garlic et dans d'autres tributaires des lacs Supérieur et Michigan, dont certains avaient été traités à un larvicide, démontrent que le début de la métamorphose peut être très variable et semble lié au taux de croissance et à la taille des larves. Une courte phase larvaire est ordinairement associée avec une croissance rapide des ammocètes, comme on le constate parfois dans des rivières où un larvicide a réduit la densité de population. La grande lamproie marine cantonnées en eau douce tend à se métamorphoser à une taille et un âge plus grands que les autres lamproies parasitaires. Durant la métamorphose, qui commence ordinairement en été, les lamproies conservent leur longueur, mais perdent du poids par suite d'une mobilisation des lipides. Il s'écoule généralement de 4 à 10 mois entre le début de la métamorphose et le début l'alimentation. La migration vers l'aval des animaux métamorphosés se fait la nuit et est influencée par le débit du cours d'eau. L'auteur compare la proportion des sexes chez les grandes lamproies marines des Grands Lacs supérieurs avec celle d'autres populations.

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A detailed account of the ecology of the larval and metamorphosing stages in the life cycle of lampreys was given a few years ago by Hardisty and Potter (1971a, b). For this reason, the current review will concentrate on those areas of ecology, or ecologically related research, which have received the most attention during the last decade. Thus, particular emphasis will be placed on recent work on the duration of larval life in both the anadromous and landlocked forms of the Atlantic sea lamprey, *Petromyzon marinus*, and comparisons will be made with estimates obtained for other species. Consideration will also be given to the changes that occur in lipid composition during larval life and metamorphosis, and their relationship to the timing of transformation and the use of fat as an energy source. Attention will also be focused on the fact that, although the onset of metamorphosis within any given population is synchronous, the time at which the subsequent downstream migration takes place is often highly variable.

Larval Lampreys

HABITATS

After fertilization, the eggs of lampreys become covered by the substrate in and around the nests where breeding has taken place (Hardisty and Potter 1971b). Hatching occurs after ~2 wk and, within a further 1–3 wk, the resultant proammocoetes emerge from this substrate and pass downstream where they burrow into silt beds in various parts of the river, especially along the more protected banks (Applegate 1950; Piavis 1971; Manion and McLain 1971). The proammocoetes take on the definitive larval form after ~5 wk, at which time they are mainly present in habitats where the substrate is composed of fine particles. Later in larval life, they are also found in areas where the average particle size is greater and, in the case of the landlocked sea lamprey, they tend to move into those slightly deeper waters where the flow is slow, such as behind rocks or logs and in eddies, and where there is often weed (Manion and Smith 1978). The maximum depth to which ammocoetes will burrow is related both to the size of the animal and the environmental conditions, with large ammocoetes retreating to as much as 18 cm below the substrate surface when there is a pronounced increase in mechanical stimulation or light intensity (Applegate 1950; Sterba 1962).

Manion and McLain (1971) found ammocoetes of *P. marinus* most abundant in habitats where 90% of the particles were less than 0.5 mm in diameter, while they were least plentiful when only 30% of the particles were below 0.5 mm. Likewise, the numbers of larval *M. mordax* were greater in two sites in which the clay and silt fraction were 20 and 5%, respectively, than in a third site where it comprised only 1% (Potter 1970). Hardisty (1944) reported that the densest larval populations of European brook lamprey, *Lampetra planeri*, were present where the substrate contained "fine silt blackened by decaying organic material." In discussing the significance of particle size, it should be remembered that substrates with a large proportion of clay, silt, and organic material will be found in those areas of the river where the water flow is slowest. In a recent study, Malmquist (1980) emphasised the role of particle size and low current velocities and water depth on the distribution of larvae of *L. planeri* in Swedish rivers.

The work of Schroll (1959) suggested that larval *L. planeri* preferred temperatures of ~12°C, while laboratory experiments on the ammocoetes of the sea lamprey have indicated that they prefer temperatures of 10–19°C (Reynolds and Casterlin 1978).

Ammocoetes are rarely found in stagnant or highly eutrophic waters, a feature that can be related to their behavior in low oxygen tensions. For example, mountain brook lamprey, *Ichthyomyzon greeleyi* (= *I. hubbsi*), ammocoetes held in the laboratory at 15.5°C and exposed to oxygen tensions of 0.9–1.3 kPa began to emerge from the substrate within a few hours (Potter et al. 1970). Thus, if for any reason the oxygen tension starts to decline drastically in the water overlying the burrows, larval lampreys can be expected to leave that particular habitat and attempt to move to more favorable sites.

MOVEMENT

The degree of dispersion of larval lampreys within a river system depends on both the hydrological and physiographic characteristics of the river. In rivers with a low profile, and where the flow is restricted, ammocoetes may spend much of their life close to those regions they had colonized after emerging from their nests (Schultz 1930; Leach 1940; Baxter 1957; M. Thomas 1962; Potter 1970). By contrast, where the gradient of the stream is relatively great and where flow is more marked, the larvae are more widely distributed and the incidence of the older year-classes increases in a downstream direction (Enequist 1937; Hardisty 1944; M. Thomas 1962).

There is now good evidence that the downstream movement of ammocoetes is seasonal and occurs mainly at night (Gritsenko 1968; Long 1968; Manion and McLain 1971; Manion and Smith 1978; Potter et al. unpublished data). In the case of the landlocked sea lamprey, Manion and Smith (1978) discovered that 92% of the larvae entering a downstream trap in the Big Garlic River, a tributary of Lake Superior, were collected between March 1 and June 30, with peak numbers occurring in April and May. Moreover, a correlation was found between the timing of this movement and the temperature of the water. The greatest amount of movement occurred as the temperatures rose from 0 to 2°C in early April to 9°C in mid-May. At temperatures above 10°C, however, the numbers declined dramatically, and by mid-June very few ammocoetes were being collected in the trap. The above correlation between water temperature and movement probably helps explain the slightly later time (May–June) recorded by Gritsenko (1968) for the peak movement of larval *Lampetra japonica* in a river in northern Russia.

The Big Garlic River study has demonstrated that water flow is an important factor in initiating movement (Manion and McLain 1971; Manion and Smith 1972). Evidence that ammocoetes move predominantly during the hours of darkness is well illustrated by the fact that 99.5% of the ammocoetes caught moving downstream in the Big Garlic River after flooding had ceased were taken at night. Moreover, even during flood conditions, 82% of the animals were collected during the hours of darkness. The "circadian" rhythm of the movement of larval ammocoetes is also shown very clearly by the data obtained for *L. japonica*. Thus, in ammocoetes of this species, a marked peak in movement was found just before 23:00, both during flood conditions and in periods of low water (Gritsenko 1968).

Manion and Smith (1978) have investigated the relationship between the pattern of movement amongst different-sized ammocoetes of the same age. They found that, although larger ammocoetes tended to move downstream more rapidly than smaller individuals, the animals caught in their trap during the early and marked periods of flooding were shorter than the mean length of the remaining members of the population. The latter finding suggests that smaller animals are less able to resist the effects of flooding, and may under normal circumstances have even been flushed into Lake Superior. That such flushing out can occur is supported by the presence of sizable ammocoete populations in offshore regions of the Great Lakes (Wagner and Stauffer 1962). If a similar situation was found, however, in anadromous species, the ammocoetes would presumably die as they are unable to osmoregulate in full-strength seawater (Hardisty 1956; Morris 1972).

One of several interesting features to emerge from the Big Garlic River study is that the numbers of ammocoetes caught in the downstream trap in the fall were relatively small compared with those taken in the spring period when both water temperature and discharge were similar. This supports the view that downstream movement is not entirely passive and completely under the influence of the scouring effects of increased freshwater discharge, and is consistent with the fact that larval landlocked sea lampreys still move in numbers in the late spring when water levels have declined to near-normal levels. Moreover, observations by Potter (1970) on *Mordacia mordax* have shown that the elevated numbers of larvae that entered an extended silt/sand bank, in the 2 mo after the rate of freshwater discharge had declined, were similar to the increased numbers that entered during and immediately after flooding. This latter finding may be explained by the following sequence of events. The ammocoetes stimulated to leave the substrate during excessive flooding, when the water level rose and fell rapidly, would have tended to burrow in any convenient site as they were flushed downstream. Since such sites were often near the water's edge where the flow was relatively slow, they would become exposed as the water levels continued to decline slightly through the ensuing weeks following the cessation of flood conditions. While this type of movement is necessary for survival, other animals which had burrowed in more protected but relatively unsuitable deeper regions of water would probably also subsequently move to more satisfactory localities.

The view that movement is not entirely passive is further supported by the fact that tagging experiments have shown that ammocoetes may occasionally move a short distance upstream (Smith and McLain 1962; Manion 1969). Although this movement presumably occurs during periods when water flow is slow, ammocoetes are capable of swimming quite rapidly. For example, M. Thomas (1962) showed that large ammocoetes of *P. marinus* could swim at 36 $\text{cm} \cdot \text{s}^{-1}$ at 4–7°C, and reported that Sholdice had recorded speeds for ammocoetes of the same species of 45 $\text{cm} \cdot \text{s}^{-1}$ at 20°C. It is unlikely, however, that such speeds can be maintained for more than a short period of time. For this reason, any pronounced movement of ammocoetes occurs predominantly in a downstream direction.

In summary, ammocoetes exhibit a pattern of movement which, although partly related to season and environmental conditions, is seen as enabling the animals to disperse within a river system and colonize new favorable habitats. However, tagging experiments have shown that ammocoetes can also remain in one area for up to 5 yr (Manion and McLain 1971).

MORTALITY

Field observations indicate that mortality at the beginning of the lamprey life cycle may sometimes be high. During spawning, various teleosts have been observed in and around the nests of different lamprey species (Schultz 1930; Hardisty 1961a; Heard 1966), and some fishes, such as minnows, logperch (*Percina caprodes*), and small rainbow trout (*Salmo gairdneri*), have been observed feeding on the eggs and very young stages of lampreys (Dendy and Scott 1953; Manion 1968). That mortality may also be high in the period immediately after the animals leave their nests is supported by the presence of large masses of small ammocoetes of *L. planeri* in the gut contents of young trout and sticklebacks (Sterba 1962). Studies by McCauley (1963) on *P. marinus* have also provided evidence that the eggs of this species would only hatch over the temperature range of 12–26°C. Thus, mortality of these stages in this species may be high in years when temperatures in the period immediately following spawning show unusual variation.

Work by Okkelberg (1922) and Hardisty (1961a) on later stages in natural populations suggest that mortality is relatively low and uniform during the rest of larval life. In the isolated population of sea lampreys in the Big Garlic River, mortality declined as the ammocoetes became larger (Manion and Smith 1978). There is little doubt that a significant factor in reducing the effects of predation is the fact that ammocoetes spend most of their time burrowed. Amongst the few reports of the ingestion of larger ammocoetes by other animals are the observations that eels feed on ammocoetes both in the laboratory (Perlmutter 1951) and in rivers (J. Thomas 1962). However, certain teleosts have also been suggested as predators by Vladykov (1949). In the detailed study of the lamprey population in the Big Garlic River, the only predator detected was a diving beetle, *Dysticus* spp., which fed on those ammocoetes that became confined in a downstream trap.

In addition to the above factors, it is highly conceivable that mortality occurs during extreme flooding, when the animal is killed either through the effects of excessive movement or by being carried into an unfavorable environment, such as salt water.

DURATION OF LARVAL LIFE AND GROWTH RATES

Structures such as otoliths, scales, and spines have proved invaluable in helping to determine the age of gnathostomatous fishes (Bagenall 1974). However, since they are absent in lampreys, estimates of the duration of larval life in the various petromyzoniform species have had to rely, except in a few experimental and atypical situations, on an analysis of length–frequency data.

Before turning to a summary of some of the estimates of the length of the larval phase, it is important to recognize the limitations inherent in the use of such information. For example, while the distribution corresponding to the first year-class might be clearly separated from the others, the distributions of each successive year-class show increasing overlap. Thus, whereas the modes for year classes three, four, and five might be relatively sharply defined, it is impossible to say with certainty that a lamprey of a particular length is a certain age, especially when its length falls in or near the "trough" between two successive modes. The modes will also tend to be better defined in populations with a relatively fast growth rate.

A second major problem is that ammocoetes not only have an asymptotic growth curve, but also tend to remain at a similar length during a relatively long period prior to metamorphosis. This part of the larval life, which has been recognized by several workers, including Gage (1928), Leach (1940, 1951), and Hardisty and Potter (1971a), has been called a "rest period" or a period of "arrested growth." During recent years, it has been demonstrated that, although in most species little or no increase in length occurs at the end of larval life, this period is used to accumulate lipid reserves as an energy source for the ensuing lengthy nontrophic period of metamorphosis (Hardisty and Potter 1971b; Lowe et al. 1973; O'Boyle and Beamish 1977; Youson et al. 1979). The presence of an "arrested growth" phase means that, even if the modes are clear for several year-classes, there is still the problem of ascertaining the time that animals spend at lengths similar to those of transforming individuals.

Data for many different populations and species, including representatives of all three petromyzoniform families, indicate that the definition of the modes in the length–frequency curves for ammocoetes varies considerably. For example, *M. mordax*, *Lampetra fluviatilis*, *L. planeri*, and *I. hubbsi* have yielded length–frequency curves in which the modes in samples were often well defined (Hardisty 1961a; Potter 1970; Hardisty and Huggins 1970; Hardisty and Potter 1971a; Potter and Bailey 1972). Moreover, although length–frequency data for the anadromous form of *P. marinus* have often displayed distinct modes representing several year-classes (Hardisty 1969; Beamish and Potter 1975), the same cannot be said for many populations of the landlocked sea lamprey in the upper Great Lakes.

Despite the above problems, a careful consideration of the more extensive data for a given species or population can often provide a useful indication of the duration of larval life. This is particularly the case where the data are based on samples from a restricted and relatively stable site in which the modes can be traced through successive length–frequency curves. The important point to remember is that the estimate of age obtained for a species at the time of metamorphosis is an "average" value, and that an inability to determine precisely the time spent by ammocoetes, at or near their size at transformation, is a complicating factor. In the following account, emphasis will be placed initially on some species which have been studied in detail and then on a description of work on the sea lamprey.

As outlined in an earlier paper in this symposium (Potter 1980), the length–frequency data for *L. fluviatilis* provide strong indications that the average duration of larval life in this species is 4½ yr (see also Hardisty and Huggins 1970; Hardisty and Potter 1971a). Although *Mordacia mordax* metamorphoses in the Moruya River in south-eastern Australia at a length ~20–30 mm greater than *L. fluviatilis*, the period of larval life is apparently shorter. The aging of *Mordacia* was based on length–frequency data for 44 consecutive monthly samples in which the mode corresponding to the year-class that hatched in 1964 predominated for much of the time (Potter 1970). The sequence of curves representing the products of spawning in 1964 strongly indicated that representatives of this species approach metamorphosing length after only 2½ yr, and often probably enter transformation after a further year. This study also showed that the mean length at transformation differed to some extent between sites within a river system and more markedly between sites in different rivers.

Recent work on *Geotria australis*, the sole representative of the other family of Southern Hemisphere lampreys, has shown that this species usually metamorphoses at ~90 mm (Potter et al. 1980). Current studies also indicate that this species increases slightly in length during the last year of life and in many cases probably enters metamorphosis at 3¼ yr of age.

The relatively short duration of larval life found in the populations of *L. fluviatilis*, *G. australis*, and *M. mordax* is thus generally correlated with a relatively small mean length of 90–130 mm at the start of metamorphosis. Moreover, as shown in an earlier contribution to this symposium (Potter 1980), species that usually metamorphose at a longer length generally have a correspondingly longer larval life. Thus, in the case of populations of *L. planeri*, in which metamorphosis takes place at ~110–170 mm, the average duration of larval life has been estimated as 6¼ yr (Hardisty 1961b; Hardisty and Potter 1971a; Potter 1980).

The length–frequency curves given by Hardisty (1969) for the anadromous form of *P. marinus* provide strong evidence that this lamprey metamorphoses at an older age than the three parasitic species mentioned previously. Thus, five distinct modes could be detected in length–frequency curves for the larvae of this species collected in the River Teme in the U.K., whereas only three predominated in *L. fluviatilis* taken from the same site. Moreover, the upper mode in the sea lamprey data was located at ~120 mm compared with 100 mm in the river lamprey. Although Hardisty (1969) did not find any metamorphosing stages of *P. marinus*, he concluded from both the length–frequency data and the pattern of gonadal development, that the duration of larval life in this species was not less than 5 yr and that for some animals it may be 6 yr.

The presence of five peaks in length–frequency curves for the River Teme is paralleled by that found by Beamish and Potter (1975) for the anadromous sea lamprey in New Brunswick, both in the Nashwaaksis River in late July and in the Miramichi River in June. Samples from the Nashwaaksis River in late July did not contain the young larvae produced by that year's spawning, which took place less than a month previously, but did contain some animals which had just entered metamorphosis. Thus, the modes in the larval representatives of the population correspond to year classes I, II, III, IV, and V. Since representatives of the year-class V will become VI in the following year, and spawning takes place at a similar time to metamorphosis (late June to mid-July), transformation is likely to begin in some animals in their 7th yr of life, i.e. when they have reached 6 yr of age. However, since in July there are always a large number of ammocoetes of the same length as those found entering metamorphosis, the time that representatives of this population of the anadromous sea lamprey spends at a length similar to that at which it will metamorphose cannot be ascertained. This problem is compounded by the fact that in the anadromous sea lamprey, it is often difficult in larger river systems to catch transforming animals and thereby obtain a reliable estimate of the ratio of metamorphosing individuals to ammocoetes of comparable length (Hardisty 1969; Beamish and Potter 1975). While this can be taken as indicating that anadromous sea lampreys remain for many years at or near their maximum length, it seems likely that it also reflects a change in habitat preference during the end of larval life which would make them more difficult to collect (Applegate 1950). However, large numbers of transforming and larval anadromous sea lampreys have been caught in Dennis Stream, a small tributary of the St Croix River, New Brunswick (Youson et al. 1977; Potter et al. 1978), where most areas could be sampled. The excellent data on the pattern of growth of the opisthonephric kidney in ammocoetes in Dennis Stream (Ooi and Youson 1976), also lends strong support to the view that, in the period immediately following metamorphosis, groups of animals are present in this population corresponding to year-classes 0, I, II, III, IV, and V.

In summary, the above data indicate that the duration of larval life of a significant number of anadromous sea lampreys is 6 yr. Although it seems highly probable that some ammocoetes do not enter metamorphosis for a further 1 or 2 yr, the proportion of metamorphosing animals to large ammocoetes in Dennis Stream in several successive years suggests that, at least in this population, the duration of larval life in most animals is 6–8 yr, as has also been proposed by Beamish and Potter (1975) to be the case in other rivers.

The structure of the length–frequency curves for the anadromous sea lamprey is paralleled by the situation found in the landlocked form of the same species in Shelter Valley Creek, a small tributary of Lake Ontario (Lowe et al. 1973), where the sea lamprey has been present since at least near to the beginning of the last century (Lark 1973). Thus six modes, which are believed to correspond to age groups 0–V, could be discerned in length–frequency curves for two separate samples from the latter part of 1969, and a similar situation has recently been reported for a population from tributaries of Lake Oneida (O'Boyle and Beamish 1977). Since the distribution of the lengths of metamorphosing animals in Shelter Valley Creek in July 1970 corresponds to those of the oldest size category caught in the latter part of 1969, some ammocoetes in this population probably entered metamorphosis when they were 6 yr old. As with the anadromous form, the period an ammocoete spends at or near its maximum length cannot be determined. However, the fact that a reasonable ratio of metamorphosing to large larvae were caught each year in Shelter Valley Creek argues that larval life is generally not extended in this river to the degree observed in the experimental population in the Big Garlic River of Lake Superior (Manion and McLain 1971; Manion and Smith 1978). Particularly pertinent in this regard is the demonstrably faster growth rate in Shelter Valley Creek (see later).

Sufficient data are now available to suggest that the anadromous form generally metamorphoses at a smaller size than the landlocked form. Thus, mean lengths of between 119 and 130 mm have been obtained for the early metamorphosing stages of the anadromous form in three different rivers in New Brunswick (Potter et al. 1978), whereas values for the comparable metamorphosing stages of the landlocked form in the Great, Finger and Oneida Lakes were generally in excess of 135 mm, and occasionally greater than 160 mm (Applegate 1950; Applegate and Brynildson 1952; Wigley 1959; Manion and Stauffer 1970; Beamish and Potter 1972; Hodges 1972; O'Boyle and Beamish 1977; Manion and Smith 1978).

Having considered estimates of the duration of larval life in long established populations of some species of lampreys, attention will now be focused on the landlocked form of *P. marinus* in the upper Great Lakes, where it has been present for only a relatively short period of time (Smith 1971). In this context, the lack of well-defined modes in length–frequency data for the landlocked form, such as those presented by Applegate (1950), contrast with those obtained for populations of *P. marinus* from both New Brunswick and a tributary of Lake Ontario. Thus, the only clear modes in length–frequency distributions for the Ocqueoc River, a tributary of Lake Michigan, were those corresponding to the first two year-classes. A possible explanation for the lack of clarity could well reside in variations in growth rate between the groups corresponding to each separate annual spawning population. That such variation can occur is borne out by Purvis' (1970) observation of differences in growth between the products of the 1960 and 1963 spawning populations of *I. fossor* in the upper Great Lakes, which he attributed to differences in the density of the ammocoete populations brought about by treatment of the streams with larvicide. Density has also been invoked by Manion and McLain (1971) and Manion and Smith (1978) for the differences they observed in the growth rate of *P. marinus* at different sites in the Big Garlic River.

In the experiment designed to ascertain the duration of larval life in a tributary of Lake Superior, a population of mature landlocked sea lampreys was isolated in 1960 in the upper reaches of the Big Garlic River which, through the presence of waterfalls, was previously inaccessible to upstream migrating lampreys (Manion and McLain 1971; Manion and Smith 1978). The larval population resulting from the spawning of these adults was then sampled at intervals over the ensuing years, both with an electric fish shocker and by collecting the animals washed downstream into a trap. Since the first downstream migrants were caught in the fall of 1965, no ammocoetes in this population started to enter metamorphosis until after the beginning of their 6th yr of life, i.e. at age V. However, the four metamorphosed downstream migrants caught in 1965 were negligible compared with the 46, 229, 398, 358, 739, 901, and 249 animals of comparable stages caught in the following 7 yr (Fig. 1). This demonstrates that in this population, representing a single year-class, animals entered metamorphosis in several successive years. The data from the above study also indicate that in the Big Garlic River, the mean length of the ammocoetes remaining in the total population of this river only increased from 111 to 129 mm between 1966 and 1972. Moreover, the maximum length in both 1966 and 1972 was virtually identical.

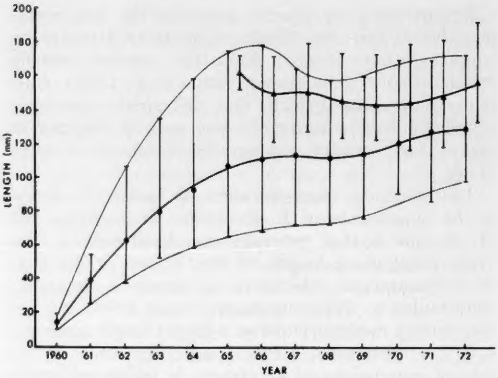

FIG. 1. Growth of the 1960 year-class of sea lamprey ammocoetes in the Big Garlic River and the lengths of the ammocoetes that metamorphosed each year. Length ranges are represented by vertical lines. ○: mean lengths of ammocoetes; ▲: mean lengths of metamorphosing stages.

The presence in the Big Garlic River of an exceptionally long period at the end of larval life is paralleled by a relatively slow growth rate during the first 5 yr of life. Thus, the larvae did not reach a mean length of 107 mm until the October of their 6th yr of life. By contrast, the mode in length–frequency curves considered as representing animals of comparable age in a short tributary of Lake Ontario at the same time of the year occurred at ~150 mm (Lowe et al. 1973). That the above difference between the populations is a true reflection of differential growth rates is borne out by clearly detectable variations in growth during the early part of life. For example, the rate of change in the mode corresponding to the 0 year-class, which can be clearly followed in the frequency curves for sequential samples in Shelter Valley Creek, shows that growth during the first months of larval life is greater in this population than in that of the Big Garlic River. Moreover, data for the growth of the first three year-classes in tributaries of Lake Superior indicate that the rate of length increase in the Big Garlic River is typical of other small streams in Lake Superior, but markedly slower than that found in large streams. This feature was attributed by Manion and McLain (1971) to differences between the temperatures in rivers of different size. It would appear that, even though Shelter Valley Creek is only 17 km in length, the ammocoetes in this stream grow at a rate more typical of that found in the larger streams of Lake Superior. Indeed, the median point in the distributions for Shelter Valley Creek in October/November 1969, taken as corresponding to year-classes 0, 1, and 11, are virtually identical with those given by Manion and McLain (1971) for animals taken from the larger tributaries of Lake Superior at the same time of the year. The differences between the rates of growth in Shelter Valley Creek and the larger Lake Superior tributaries and those in the Big Garlic River and smaller Lake Superior tributaries are particularly well illustrated by the fact that in the fall the respective mean lengths of ammocoetes of year-class II were ~90 mm in the former rivers and only about 60 mm in the latter.

Despite the fact that the mean length of 5-yr-old ammocoetes in the Big Garlic River is ~40 mm below that of similar aged animals in Shelter Valley Creek, the modal length of individuals at the start of metamorphosis is very similar in the two populations (about 140–145 mm). This implies that the timing of metamorphosis is related to length, or some factor closely related to length, and helps to explain why the population in the Big Garlic River metamorphoses over so many years. For example, whereas in 5 yr, many individuals in Shelter Valley Creek have reached lengths typical of those exhibited by metamorphosing animals, the slower growth rate in the Big Garlic River will mean that in general the ammocoetes in this river will require a longer period to attain a comparable size.

The above hypothesis is consistent with the results of a comparison of the time of the first metamorphosis and the growth rate of larvae within populations living in streams that had been previously treated with TFM larvicide (Purvis 1979). Thus, there was some evidence that a few ammocoetes entered metamorphosis as early as their 4th (age III) or 5th yr (age IV) of life in rivers in which the growth rate was rapid, whereas the onset of metamorphosis was delayed until at least the 8th yr when growth was very slow. In rivers with intermediate growth rates, ammocoetes first started to enter metamorphosis in their 6th yr of life. The main feature of these studies is the frequency with which a mean length of ~140 mm was present in the samples of transforming animals and the fact that on only one occasion did an animal enter transformation at less than 120 mm. There was also an indication that the size at transformation was greater in those rivers in which the growth rate was rapid, despite the fact that animals entered transformation later in rivers where growth was slow. It is also feasible that the "arrested growth phase" or "rest period," during which the animal accumulates lipid and does not increase markedly in length, may vary from several years in those rivers where the growth rate is slow to a very short period in those with rapid growth. In view of the fact that the biomass of the animal increases over this terminal period of larval life, it is probably best to refer to this phase as a "premetamorphic period," rather than an "arrested growth phase" or "rest period."

The very slow growth rates of animals above ~70 mm in the Big Garlic River (Fig. 1) would provide one reason why Manion and Smith (1978) found, after the first few years of their study, a great degree of overlap between the length–frequency distributions for successive annual samples of ammocoetes of the same age. Moreover, this overlap has presumably been exaggerated by their pooling of the length data for animals from different areas on the river, which they have shown to exhibit different growth characteristics. Overlap may also have been increased since, during the early part of the study, ammocoetes caught in the downstream trap, presumably originating from different areas, were deposited back upstream (Manion and McLain 1971). A factor that may have affected growth rates is the gradual decline in density that must have taken place in this single year-class population due to mortality amongst larvae and the migration downstream of metamorphosed individuals.

For the above reasons, it would appear that, while the data collected from the experimental population in the Big Garlic River has added considerably to our knowledge of the ecology of larval lampreys, some of the remarks made by Manion and Smith (1978) questioning the validity of using length–frequency data for determining the age structure of populations of sea lampreys in the Great Lakes are not universally applicable. In fact, whether or not length–frequency curves can be used appears to depend to a very large degree on the growth rate and the stability both of the population in a river system and of the site from which the samples were taken. The above view is based on comparisions between data for the Big Garlic River and that found in such rivers as Shelter Valley Creek in Lake Ontario (Lowe et al. 1973). As pointed out by Manion and Smith (1978), length–frequency data for landlocked sea lampreys in such rivers as the Big Garlic, and possibly also other small tributaries of Lake Superior in which growth is slow, are of little use for estimating the duration of larval life. By contrast, length–frequency curves have also demonstrated that in data for rivers such as Shelter Valley Creek, where growth rates were much more rapid, five or six relatively well-defined modes were often present. Thus, length–frequency data can be used to ascertain how long ammocoetes generally take to reach metamorphosing length in sea lamprey populations collected from a relatively stable and restricted area of at least one tributary of Lake Ontario in which the growth was relatively fast.

In the context of the above comments, it may be significant that sea lamprey populations have been established in Lake Ontario for a relatively long period of time (Lark 1973), whereas those of the upper Great Lakes are of very recent origin (Smith 1971). Thus, the pattern of growth, which is apparently related at least in part to density, is likely to be more consistent in the longer established populations, and thus lead to more clearly defined modes in length–frequency curves. Moreover, it is clear that the sex ratio in the Big Garlic River population is not typical of that found in long established populations, including those of the sea lamprey which have not been exposed to larvicide treatment (see section on sex ratios).

GROWTH RATES

Although the growth rate of larval landlocked sea lampreys in the Big Garlic River is slow, it is clear from the pattern of annual increases in length during the first 5 yr that growth in this river is asymptotic (Fig. 1; Hardisty and Potter 1971a). A similar situation was found in *M. mordax*, which, however, undergoes much greater annual increases in length (Potter 1970). The data for this latter species also demonstrate that growth is seasonal, with most of the increase in length taking place during the warmer months of the year. A similar situation pertains in many holarctic species (Potter and Bailey 1972; Lowe et al. 1973; Beamish and Potter 1975; O'Boyle and Beamish 1977). Moreover, there is some evidence that lengths can decline in the winter months (M. Thomas 1962) or during prolonged and severe flooding (Álvarez del Villar 1966).

There is now data to suggest that in some species the growth rate of female ammocoetes may be slightly greater than that of males. For example, on two separate occasions Purvis (1970) found that after ~3 yr of age the female ammocoetes of *I. fossor* were 4–5 mm longer than the males. The females are often longer at the onset of transformation. Thus, differences have been recorded between the lengths of the two sexes in *P. marinus* (Applegate and Thomas 1965; Purvis 1979a) and in *L. fluviatilis* and *L. planeri* (Bird and Potter 1979b). Furthermore, even though the means differed by less than 4 and 7 mm in the parasitic and nonparasitic species of *Lampetra*, respectively, the differences were significant at the 95% level. By contrast, no significant difference was found between the male and female metamorphosing stages of *G. australis* (Potter et al. 1980). Although female ammocoetes sometimes grow more rapidly than males, the males of at least some species apparently start metamorphosing at an earlier age. Direct support for this view is provided by the observations on known age populations of *I. fossor* and *P. marinus* (Purvis 1970; Manion and Smith 1978; Purvis 1979). It is also supported by the fact that in metamorphosing stages the males are slightly more abundant than females (Bird and Potter 1979b; Potter et al. 1980; see also section on sex ratios).

The data collected for the population of landlocked sea lampreys in the Big Garlic River suggest that, if it reflects the typical situation found in small tributaries of Lake Superior, the populations from such localities are almost certainly at a disadvantage compared with those in larger river systems where the temperature regimes are warmer. An excessively long duration of larval life is thus seen as reflecting an inability of the ammocoete to grow and accumulate substantial lipid reserves at a sufficiently fast rate to facilitate metamorphosis within a period of 6–8 yr, which is considered more representative of the time typically taken in warmer areas and among long established populations.

The information presented in this and the previous section has shown that the growth rates and duration of the larval phase in the landlocked sea lamprey can vary greatly. Although there is now evidence that such variation can exist even within a single river system, the degree of variation tends to be much greater between rivers with conspicuously different environmental characteristics. Thus, growth is faster in larger and warmer rivers, which are also probably more productive and stable, than in smaller and colder rivers (Manion and Smith 1978). The results of eliminating larvae in rivers with larvicide, and following the increase in length of the newly established population, have also provided strong evidence that growth rates are greatest when densities are lowest (Purvis 1979, 1980).

Ammocoetes of *M. mordax* were found to move during each month into an area after a fish shocker had been used to remove once monthly the larval population (Potter 1970). When the animals were replaced each month, however, the numbers in the population remained relatively constant, suggesting that ammocoetes may regulate their density. Because growth is apparently reduced in high densities, it would appear that the amount of available food, and possibly also other factors, such as the type of substrate, may limit the extent to which a site may be colonized by larval lampreys.

LIPID COMPOSITION

The amount of lipid present at the beginning of metamorphosis has been found to be very similar in populations representing three different species of lampreys. Thus, lipid values equivalent to 13.5, 14.2, and 14.6% of the wet body weight have been recorded for landlocked *P. marinus*, *L. fluviatilis*, and *L. planeri*, respectively (Lowe et al. 1973; Moore and Potter 1976). These similarities are particularly striking when the differences in the mode of life of the postlarval stages of these species are considered. Thus, whereas both the river lamprey and the landlocked sea lamprey have an adult parasitic phase, feeding takes place in the sea in the former and in lakes in the latter. By contrast, the brook lamprey has eliminated feeding entirely from the period following the start of transformation. The significance of the large lipid stores accumulated at the end of larval life can be related to the need for the animal to possess sufficient energy reserves for the ensuing nontrophic period. During this time, such reserves are used for maintenance and the radical morphological and other changes that take place during metamorphosis, prior to the assumption of either parasitism in *L. fluviatilis* and *P. marinus* or sexual maturity in *L. planeri*.

Despite the similarity in the lipid values for *P. marinus* and *L. planeri*, the pattern by which fat is accumulated during the larval phase varies markedly in the two species. Although in the sea lamprey, the relative amount of fat rises annually in the early summer, the level remains for most of the time more or less constant at ~4% of the wet body weight until the animal reaches a length similar to that at which metamorphosis takes place (Lowe et al. 1973). The large buildup in lipid that occurs towards the end of larval life is also well illustrated by histological studies, which have shown that at this time great increases in fat occur in such areas as the fat column, myosepta, nephric fold, beneath the skin and around the body cavity (Youson et al. 1979). Biochemical studies by O'Boyle and Beamish (1977) have also shown that the lipid accumulates in the muscles during the period prior to metamorphosis, a process which these workers related to changes in the activity of certain enzymes. The relative amount of fat in the brook lamprey also increases during the spring and early summer, but unlike the sea lamprey it increases annually, with the result that, at the time when transformation is taking place, animals just below metamorphosing length have lipid values approaching those found in the earliest stages of metamorphosis (Moore and Potter 1976). It can thus be postulated that the lipid levels generally take a longer time in large ammocoetes of *P. marinus* to reach those characteristic of the early stages in transformation than is the case in *L. planeri*. Such a difference may account for the apparently more protracted period found at the end of larval life in *P. marinus* than in *L. planeri* and other species. Moreover, since the conditions in the Big Garlic are not apparently optimal for growth and lipid accumulation, this would also help explain why many ammocoetes take such a long time to enter transformation in this particular river system.

SEX RATIOS

Before turning to the sex ratios in larvae, it is beneficial to consider first the comprehensive data for adults and metamorphosing stages.

Several studies have shown that spawning populations of lampreys, and in particular those of the nonparasitic species, contain a preponderance of males (Dean and Sumner 1898; Young and Cole 1900; Lubosch 1903; Reighard 1903; Loman 1912; Schultz 1930; Ivanova-Berg 1931; Damas 1950; Applegate 1950; Zanandrea 1951, 1961; Eglite 1958; Abakumov 1960; Hardisty 1961a Lohnisky 1966; Hubbs 1971; Bird and Potter 1979b). During recent years, however, evidence has been obtained which suggests that the males may not predominate to such a degree at other stages in the life cycle. This view is based on the fact that the sex ratio of animals caught during metamorphosis, and during the upstream migration of representatives of "stable" populations, were generally closer to parity. For example, sex ratios of 1.0♀:1.20♂ and 1.0♀:1.21♂ have been obtained, respectively, for metamorphosing representatives of *L. fluviatilis* (Bird and Potter 1979b) and *G. australis* (Potter et al. 1980). Moreover, in contrast to an overall sex ratio of 1.0♀:2.0♂ obtained by Hardisty (1961a) for pooled data for 13 consecutive spawning seasons in the case of *L. planeri*, Dines (1973) found in several different populations of this species caught during metamorphosis a sex ratio closer to those obtained in the two species listed above. Likewise, studies on the sea lamprey caught during its upstream migration have yielded 1.0♀:1.18♂ for the anadromous form in New Brunswick (Beamish and Potter 1975) and of between parity and 1.0♀:1.31♂ in five successive annual spawning migrations of the landlocked form in a tributary of Lake Ontario, prior to the time when the rivers of this lake were treated with larvicide (Potter et al. 1974). The above data also show a relatively close correspondence to the pooled sex ratio obtained for the typical forms of *L. fluviatilis* (1.0♀:1.06♂) and *M. mordax* (1.0♀:1.07♂) caught early in their spawning run (Abou-Seedo and Potter 1979; Potter et al. 1968).

The fact that metamorphosing and upstream migrant populations apparently show a less pronounced excess of males than spawning populations may be due to differences in the pattern of movements on the spawning grounds. For example, since males of *L. planeri* tend to spend a longer time in the vicinity of the nests than females (Malmquist 1978; Bird and Potter 1979b), samples taken from the spawning beds would tend to show an exaggerated sex ratio in favor of the males.

The question now raised is whether a relationship exists between the slight excess of males found after the start of metamorphosis and the situation existing in larval populations. In *P. marinus* the proportion of females is greater than males amongst the largest ammocoete size-group (Hardisty 1965), and in metamorphosing *I. fossor*, *L. fluviatilis*, and *L. planeri* the females were slightly longer than the males (Churchill 1947; Bird and Potter 1979b). As pointed out earlier this is consistent with the fact that males tend to metamorphose earlier than females.

It would thus appear that the slight excess of males in postlarval stages may be attributable to the increased mortality found amongst female ammocoetes as a result of the longer duration of larval life in this sex. Moreover, it has been suggested that the correlation found between large spawning populations and the presence of a high proportion of males can be related to an earlier metamorphosis of a relatively larger number of males than in years when abundance was not as great (Hardisty 1961a).

The consistent finding of a slight excess of males in the metamorphosing and spawning-run stages of long-established populations contrasts with the remarkable variation in sex ratios found in landlocked sea lampreys in the upper Great Lakes (Smith 1971). Thus, the upstream migration of landlocked *P. marinus* were characterized by a large excess of males during the period of rapid population expansion, followed by a decline in males in the years when the numbers were falling. This point is illustrated by the fact that the percentage number of males in Lake Huron was 72.2% in 1951 and 46.0% in 1969 (Smith 1971). Moreover, in Lake Superior, the proportion of males fell to only 26.7% in 1969 from a high of 69.6% in 1962. Marked variations in sex ratios have also been found in downstream migrant populations of the landlocked sea lamprey (Applegate and Thomas 1965; Purvis 1979a). These variations probably reflect the "unstable" nature of the populations compared with those long established populations that had not been exposed to larvicide for which data were given earlier. This view is supported by the fact that the typical sex ratios found in the Humber River of Lake Ontario prior to larvicide treatment (Potter et al. 1974) contrast with those being obtained in Lake Ontario following the use of TFM (Torblaa and Westman 1980).

The sex ratio of the landlocked sea lampreys in the Big Garlic River does not conform with the pattern found in other species. Thus, in contrast to the usual slight predominance of males among transforming stages, the sex ratio in the large samples of metamorphosed individuals taken between 1967 and 1972 was always less than 1.0♀:0.35♂ and reached a minimum of 1.0♀:0.15♂ in 1972. Moreover, even in 1966, when only a very small proportion of this single year-class population had undertaken metamorphosis, the number of female ammocoetes was nearly five times that of the males. The presence in 1966 of a large excess of female ammocoetes in the single year-class in the Big Garlic River should not be confused with the situation in multi-year-class populations in which females also predominate amongst the larger larvae as a result of the earlier metamorphosis of males (see earlier in this section).

Metamorphosis

HABITATS

In many species, the early stages of metamorphosis have been found in large numbers in the same sites as ammocoetes of all sizes (e.g. Hardisty and Huggins 1970; Potter 1970; Potter and Bailey 1972; Potter et al. 1980). There is also evidence that, although during the first few weeks of metamorphosis transforming animals are relatively more sedentary than ammocoetes, they then move out of slow flowing areas into regions where the substrate is coarser and water flow is faster (Potter 1970; Potter and Huggins 1973). Laboratory experiments also suggest that, following the completion of metamorphosis, *L. fluviatilis* burrows less frequently and lies hidden during the day between pebbles and other structures (Potter and Huggins 1973). While such trends are apparently exhibited by the sea lamprey in small streams (J. H. Youson, University of Toronto, personal communication), the evidence presented earlier indicates that, in the period prior to metamorphosis, the large ammocoetes of the sea lamprey may start moving to sites other than those normally characteristic of the larva (Applegate 1950; Beamish and Potter 1975; Manion and Smith 1978).

SEASONAL INCIDENCE

During the last 2 or 3 yr, detailed studies on the stages in the metamorphosis of lampreys have shown that the very earliest external signs of transformation can only be detected after very careful morphological examination. The most conspicuous of the initial external alterations, which are essentially the same in both northern and southern hemisphere species, include small changes in the appearance of the eye and a slight enlargement of the "lips" of the oral hood (Potter et al. 1978; Bird and Potter 1979a; Youson and Potter 1979; Potter et al. 1980). Thus, although within a population external metamorphosis is relatively synchronous, and the first two stages are generally each of relatively short duration, it seems likely that some of the early work on metamorphosis may not always have recognized the point at which the first changes are incipient. For example, two metamorphosing stages have now been described for the sea lamprey (Potter et al. 1978; Youson and Potter 1979) that are clearly earlier than the first stage originally described for this species by Manion and Stauffer (1970). For the above reasons, caution should be exercised in placing too great a reliance on the precise time when metamorphosis is said to be initiated in some previous studies.

Despite the above relatively minor reservations, there is now a wealth of information to indicate that in most holarctic species transformation generally begins during the summer months (see Hardisty and Potter 1971b). Moreover, the recent detailed investigations of the early stages in the metamorphosis of *P. marinus* in New Brunswick and of *L. fluviatilis* and *L. planeri* in British rivers, provide confirmation that, although there is far greater variability between years and populations in the latter two species, the first two stages of *Lampetra* spp. are still generally only present between the end of June and the end of August (Potter et al. 1978; Bird and Potter 1979a; Youson and Potter 1979).

The data in these latter studies have also emphasized the highly synchronous nature of the onset of metamorphosis in any given species within a particular river system. While this synchrony in external metamorphosis is to a large extent sustained in subsequent stages, it is also apparent that the main changes in morphology occur during the first 2 mo of metamorphosis. A probable explanation for the rapidity of these early modifications may reside in the fact that the animals are vulnerable at this stage in their life cycle (Potter 1970). For example, since alterations are necessary to permit a change in the respiratory water intake from a unidirectional to a tidal flow, the animal may have to rely at some point on gaseous exchange through the skin, rather than on the more efficient mechanism of using gills (Randall 1972; Hardisty and Potter 1971b; Potter et al. 1978).

In the Southern Hemisphere, metamorphosis is initiated in parasitic lampreys between mid-January and early March, i.e. at an equivalent time of the year to that of holarctic species. This applies both to *Mordacia mordax* in south-eastern Australia (Potter et al. 1968; Potter 1970) and to *G. australis* in Tasmania, south-western Australia (Potter et al. 1980) and New Zealand (Maskell 1929). However, in the Moruya River in New South Wales, metamorphosis in the nonparasitic *M. praecox* starts in November, ~3 mo before that of *M. mordax*, its presumed ancestral species (Potter 1968, 1970). This difference between the two members of the only paired species described for the Southern Hemisphere therefore contrasts with the close similarity in timing found in such holarctic paired species as *L. fluviatilis* and *L. planeri* (Bird and Potter 1979a).

Despite the synchronous nature of the start of metamorphosis in any given population, the precise time at which the first changes can be observed may vary with locality. For example, the onset of transformation occurs earlier in *L. planeri* from some Welsh rivers than in those of southern England (Dines 1973; Bird and Potter 1979a), and likewise changes in *M. mordax* are incipient in Tasmania earlier than those found in south-eastern Australia (Potter et al. 1968; Potter 1970). Although transformation was first detected in both species in those rivers with the lower temperature regimes, there is evidence that within any single river system metamorphosis is initiated earliest in years when there has been an early spring (Bird and Potter 1979a). Moreover, in the laboratory, metamorphic changes occurred first in those animals exposed to the higher of two temperature regimes (Potter 1970). Thus, the onset of metamorphosis may be related more to the pattern of change in temperature, rather than to a universally applicable critical temperature. Such a view is consistent with the very close correspondence found in the time at which in each year anadromous sea lampreys in New Brunswick enter metamorphosis. This occurs in mid-July following a large and rapid rise in temperature after the ice starts to break up in May (Potter and Beamish 1977).

Temperature has also been invoked by Purvis (1980) as an important factor in the incidence and timing of metamorphosis on the basis of experiments carried out with the ammocoetes of a known age-class of *P. marinus*. Larvae were taken from the Big Garlic River in the spring and placed either in the laboratory or in Lake Superior. Purvis found that the incidence of transformation in the summer was 11 times greater in the animals held in the laboratory than in those in Lake Superior, when the respective temperatures were 20–21°C and 7–11°C. Moreover, an intermediate situation was present in the population that was left in the Big Garlic, where the temperature at transformation was 14–16°C. Some caution must be exercised in drawing conclusions from these results in view of the variability in many aspects of the environmental conditions to which the three groups were subjected.

Another environmental factor which might influence the initiation of metamorphosis is the marked change in day length found in the months immediately prior to transformation. That such a factor might be of importance would be consistent with the presence in lampreys of a well developed pineal (Eddy 1972) and with the observation that in *L. planeri* pinealectomy inhibits metamorphosis (Eddy 1969).

DOWNSTREAM MIGRATION

The synchronous nature of the sequence of developmental changes that take place during metamorphosis in *G. australis* is paralleled by the fact that in south-western Australia the downstream migration of this species occurs over a relatively restricted period of time. Thus, in three successive years, the fully metamorphosed *G. australis* embarked on their downstream migration to the sea during either July or early August (Potter et al. 1980). In south-eastern Australia, however, considerable variability was found between years in the period when *M. mordax* finally left the river system, the time ranging from August to November (Potter 1970). Even more dramatic differences have been observed in the river and sea lamprey. Thus while these two species often migrate to lakes or the sea in the fall, large numbers sometimes remain in the river systems until the following spring (Applegate 1950; Potter and Huggins 1973; Potter and Beamish 1977; Bird and Potter 1979a).

A probable explanation for differences between populations and species can be obtained by considering the relationship between the degree of development of the animal, the time of the movement, and the prevailing environmental conditions. Thus, in south-western Australia, the downstream migration of *G. australis* took place when freshwater discharge reached high levels and the animals had just attained juvenile adult characters. Although the downstream migration of *M. mordax* in southern New South Wales is also related to marked increases in freshwater discharge, the time at which such conditions are present is much more variable. Thus, when significant flooding took place in August, most of the animals moved to sea, but when water levels remained relatively constant during the late winter and spring, a number of young adults were still found in the river system many weeks later (Potter 1970).

The markedly bimodal nature of the timing of the downstream migration sometimes found in sea lampreys is well illustrated by Applegate's (1950) data for the Ocqueoc and Carp Lake rivers, which show a major movement occurring in both the fall and spring. A plausible hypothesis for this phenomenon can also be constructed by invoking environmental conditions and the degree of development of the animal. Thus, if an animal has fully metamorphosed in the fall before temperatures have fallen to values approaching 0°C, and is exposed to the stimulus of increased flow, it is likely to start migrating downstream. If, however, the animal has not completed metamorphosis by the time "winter" conditions have developed, or has not received a sufficiently strong environmental stimulus to move, it will generally have to wait until the following spring before rising temperatures and discharge rates provide conditions conducive for migration. Data on *M. mordax* showed that the migration of metamorphosed individuals of this species began earlier from an upstream than downstream site, a feature which is probably attributable to the greater rate of flow in the former region (Potter 1970).

The downstream migration of sea lampreys at two entirely different times of the year may be of considerable value to this species. The animals migrating in the fall are at an advantage over those that migrate in the spring through the possession of larger lipid reserves and the opportunity to feed earlier. However, if the fall migrants are exposed to deleterious effects during the subsequent winter months, the population of young feeding adults can subsequently be boosted by an influx of fully metamorphosed lampreys in the following spring. Although in British rivers the river lamprey also moves to sea in the autumn and spring (Potter and Huggins 1973; Bird and Potter 1979a), this species has also been observed migrating during the early winter in France (Léger 1920).

It is clear from the above studies that the main trigger for stimulating the downstream migration is a marked increase in freshwater discharge. Since metamorphosed animals are often found in faster flowing regions of the river (Applegate 1950; Potter 1970), it follows that after being stimulated to emerge from the substrate during flood conditions, they will be rapidly transported towards their lacustrine or marine adult environment.

There is evidence that the migration downstream occurs predominantly at night, at least in the case of *L. fluviatilis* (Potter and Huggins 1973), *L. tridentata* (Gritsenko 1968), *P. marinus* (Léger 1920; Applegate 1950), and *G. australis* (Potter et al. 1980). Since in these studies downstream migrants were invariably caught during darkness, they probably burrow or move into protected areas during the daytime. Such a view is consistent with laboratory observations on fully metamorphosed *L. fluviatilis* exposed to a light/dark regime paralleling that found in the field at the time of capture (Potter and Huggins 1973). The animals were generally found swimming in the aquaria only during darkness, while the use of large pebbles as a source of cover was extensively employed in periods of light. In the case of *M. mordax*, which is an unusual species in that their adults burrow (Potter et al. 1968), the downstream migrants enter coarse substrates in the faster flowing regions of rivers during the day (Potter 1970). Fully metamorphosed *L. tridentata* were found by Gritsenko (1968) to migrate downstream in midchannel and throughout the water column, whereas ammocoetes that had been flushed out were present along the banks of the river.

Applegate (1950) and Applegate and Brynildson (1952) suggested that the downstream migration is passive. This view was based on their observations that lampreys rarely attempted to accelerate their downstream movement, that their movements were casual, and that individuals were occasionally seen drifting tail-first. The passive nature of this migration, and its relationship to increased freshwater discharge, parallels to some degree the seawards movement of salmon smolts, the latter representing in many ways a comparable stage in the life cycle of an entirely different anadromous vertebrate (Jones 1959; Hoar 1976). A further parallel between some species of salmon and lampreys is found in the "circadian" nature of the migration. Thus, Neave (1955) has described how migrant pink salmon hide under stones during the day, although later work has shown that with schooling experience this behavioral trait disappears (Hoar 1976). The suggestion made earlier that rising water temperatures in the spring might act synergistically with any concomitant increases in water level to promote a seawards migration would parallel results obtained for salmonids (see Solomon 1978). Hoar (1976) has also suggested that in salmonids, the longer a smolt remains in the river, the greater the degree of physiological change towards the adult condition and the more receptive it is to environmental stimuli. It may thus be significant that metamorphosed anadromous sea lampreys that had been in the river system for a long period were observed migrating during the day as well as the night (Applegate and Brynildson 1952). In other words, these lampreys had become so responsive to the stimuli that initiate migration that light or some associated factor no longer inhibited a daytime movement.

DURATION OF METAMORPHOSIS

The contrast in some species, between the variability in the timing of the downstream migration and the synchrony of the metamorphic changes, highlights the problem of defining precisely when metamorphosis is completed. Manion and Stauffer (1970) have suggested the use of the following four criteria for the sea lamprey. (1) Emergence from substrate; (2) downstream migration in the rivers (also adopted by Gage (1928), Applegate and Brynildson (1952), and Wigley (1959)); (3) oral blood openings of 8–9% of the total body length (also used by Vladykov (1949)); and (4) the beginning of parasitic feeding. However, there is clearly a problem in invoking this set of cumulative characters as only one or two of these features might be exhibited by the animal at any one time, especially as some require the presence of specific stimuli.

Although there is great variability in the timing of the downstream migration in some populations, an estimate of the minimum duration of metamorphosis can be obtained from data on when the animals have apparently developed the morphological characters of young adults and embarked on a downstream migration. Since *L. fluviatilis* generally begin metamorphosis in July, and young animals with fully developed dentition have been caught in the Severn estuary (U.K.) as early as late October, this species apparently requires at least 3½ mo to reach the stage when it is ready to embark on its marine trophic phase (Bird and Potter 1979a). At the same time, some of the characteristic metamorphic changes, such as the development of an open foregut and the switch from larval to adult haemoglobins, are not completed in some *L. fluviatilis* until several weeks later (Hardisty et al. 1970; Potter and Brown 1974).

Similar variability to that found in the timing of the final metamorphic changes in *L. fluviatilis* have been observed in the degree of development of the lingual laminae of the landlocked sea lamprey by Lennon (1954), who concluded that metamorphosis had not been completed in most animals migrating downstream in the fall and that feeding would generally not be possible until the following spring. These findings are not paralleled by the situation found in anadromous sea lampreys caught in New Brunswick, which by December showed adult characters and were invariably capable of feeding in the laboratory when provided with suitable teleost hosts (Youson and Potter 1979). Thus, if one takes the first time when these sea lampreys develop juvenile adult characters and have the ability to feed parasitically as representing the end of metamorphosis, it would seem reasonable to suggest that the changes to an adult form are completed in the anadromous sea lamprey by the late fall or early winter.

In view of the apparent differences in the rate of some of the final and crucial metamorphic changes, both between and within species, future detailed work on the precise time when adult characters are developed in a variety of individuals would clearly lead to a greater understanding of lamprey metamorphosis.

WEIGHT, LENGTH, AND CONDITION FACTORS

During metamorphosis, the mean lengths of *P. marinus* and *G. australis* remain relatively constant, whereas their weights undergo a significant decline (Potter et al. 1978, 1980). In a laboratory experiment, eight landlocked metamorphosing sea lampreys were found by Manion and Stauffer (1970) to increase very slightly in length between the earliest and latest stages they investigated. This feature can be clearly related to the massive enlargement that takes place in the preorbital region of this species as it assumes the characteristics of the adult (Potter et al. 1978). The loss in body weight in both species reflects the fact that, since the animal is not feeding, it is utilizing energy stores, particularly lipid, both for maintenance and for the various changes that are taking place. The loss of body weight (W) relative to length (L) is shown even more clearly by examining the pronounced downward trend that occurs during metamorphosis in the condition factor, namely (weight in g/length in mm^3) $\times 10^6$ (Ricker 1975). For example, it declined in *P. marinus* from 1.62 at stage 1 of metamorphosis to 1.32 at stage 7 (Potter et al. 1978).

LIPID STORES AND UTILIZATION

There can be little doubt that the accumulation of large lipid reserves (about 14% of the wet body weight), by the time when metamorphosis starts, has almost certainly been a major factor in permitting the development of a flexible period between the end of larval life and the onset of feeding. Thus, although lipid is used both as a general source of energy, and to aid protein synthesis (O'Boyle and Beamish 1977), lipid levels in landlocked *P. marinus* are still high (about 7%) in the fall when many members of the population are known to migrate. Similar levels were also found in *L. fluviatilis* in the following February (Moore and Potter 1976), just prior to the time when the last remaining downstream migrants of this species move to sea (Potter and Huggins 1973). The retention of an appreciable quantity of lipid is probably important as it provides an energy source for the animal during its movement towards the sea. However, in populations of the anadromous sea lamprey in New Brunswick, which do not start feeding until 10 mo after the onset of metamorphosis, the lipid may become depleted to such an extent that the animal has to resort to protein catabolism. In such animals caught in Washademoak Lake, a tributary of the St. John River, the amount of lipid had declined in May to levels equivalent to only 1.0% of the animals wet body weight (Beamish et al. 1979). That such remaining lipid is all, or almost entirely phospholipid, is supported by a histological study using specific fat-staining techniques (Youson et al. 1979). Moreover, this latter study showed that the musculature exhibited signs of wasting, which indicates that protein had been utilized. The absence of neutral lipid as an energy source in those lampreys that do not enter the sea until nearly a year after the onset of transformation may be related to the fact that these animals eventually migrate only after feeding on upstream migrating teleosts in freshwater. This view is based on the assumption that the presence of a reasonable store of fat is essential to enable the animal to cope with the demands of a downstream migration, during which it does not feed. In other words, the short period spent feeding on upstream migrating teleosts is seen as a method by which lipid stores can be replenished. That such replenishment occurs is borne out by a comparison of the fat in a young adult sea lamprey of about 5.0 g, which is believed to have been feeding for a short period, with a smaller very emaciated animal of only 1.5 g which had presumably not yet fed (Youson et al. 1979).

SALINITY TOLERANCE

Fully metamorphosed anadromous sea lampreys, which were caught in May in freshwater prior to their initial movement to sea and at a time when they had just started feeding on upstream migrating teleosts, are capable of osmoregulating in salinities of 34‰ (Beamish et al. 1978). Experiments in which downstream migrant representatives of other species have been transferred to seawater of various concentrations suggest that these individuals were capable of osmoregulating in full-strength seawater (35‰). Thus, in both *L. fluviatilis* and *G. australis*, acclimated for 4 d at first 12 and then 24‰, the mortality after a further 4 d at 35‰ was less than 15% (Potter and Huggins 1973; Potter et al. 1980). Furthermore, over 65% of the animals at this stage were also capable of surviving direct transfer from 0 to 35‰.

Some Conclusions and Comparisons

The data collected for various aspects of the biology of the landlocked *P. marinus* can now be used to provide a hypothetical scheme for the sequence of events that lead up to and influence the timing of metamorphosis in this lamprey. The following features have been considered to be of particular relevance.

1) The growth rate varies between and within rivers.
2) The mean length at metamorphosis is generally about 140 mm, although several greater and a few smaller mean lengths have been recorded.
3) The age at which metamorphosis is initiated is related both to the size and growth rate of the animal.
4) Lipid levels remain at about 4% of the wet body weight until the ammocoete reaches a length comparable to that at which it will enter metamorphosis when they rise to 14%.
5) Alterations in the activity of certain enzymes during the terminal part of larval life result in the animal changing from predominantly protein to lipid anabolism.

Under conditions favorable for feeding and growth, the larvae of the landlocked sea lamprey appear to take an average of 5 yr to reach a length similar to that of transforming individuals. At this time, the ammocoetes have reached both the necessary length and age for the metabolism of the animal to be switched towards the accumulation of lipid. Whether or not the animal enters metamorphosis in the following year may then depend on how successful it has been in increasing the lipid content from values corresponding to 4% of the wet body weight, as is found throughout most of larval life, to ~14%, the amount present at the start of metamorphosis. In the case of Shelter Valley Creek, which is considered to provide good conditions for feeding and growth, the significant number of metamorphosing animals taken in samples at appropriate times of the year suggest that most larvae metamorphose within 1–3 yr of reaching metamorphosing length. From the data given by Manion and McLain (1971) and Purvis (1979a, b) for growth rates in different tributaries of Lake Superior, a similar situation also probably exists in the larger, warmer, and more productive rivers of the Great Lakes. Under exceptionally good conditions for growth, which probably include those which, through the use of TFM, have led to greatly reduced densities, animals may reach ~140 mm in 3 yr and continue to increase in length. A few of these animals may enter metamorphosis in their 4th or 5th yr of life having accumulated lipid rapidly.

In contrast to the situation described above is that found in rivers which are less conducive to growth, such as the Big Garlic River and the smaller, colder tributaries of Lake Superior. In these river systems, it is apparent that a large number of animals take longer than 5 yr to reach ~140 mm, which is generally the minimum length at which the change from protein to lipid anabolism is initiated. Moreover, in the Big Garlic River, where some ammocoetes remained as larvae for 18 yr, it seems likely that some ammocoetes would never have attained a condition that would have enabled them to enter metamorphosis.

One interesting point to arise from the above hypothesis is that it implies that larval lamprey populations in the larger, warmer, and more productive streams are probably at a considerable advantage over those which live in less favorable environments for feeding and growth. Such a view is based on the premise that, because of the shorter duration of larval life, mortality will almost certainly be lower.

From the above account, the flexibility of the duration of the larval phase is envisaged as being crucial to permit the animal to attain a sufficiently large size and to develop a large potential energy source in the form of lipid. Such a fat store is particularly important in the case of the sea lamprey as it sometimes does not start feeding until nearly a year after the onset of transformation. The adaptability of lampreys is further illustrated by the indications that, if the fat stores become excessively depleted, the animal is able to resort to protein catabolism.

Some of the aspects of the biology of the landlocked sea lamprey discussed above provide an interesting comparison with those obtained for other species. For example, landlocked *P. marinus* metamorphose at a large body size and has an unusually long larval life compared with those of other parasitic lampreys, which generally metamorphose at lengths of 90–130 mm after an average larval life of 3½–4½ yr. The protracted larval life is almost certainly associated with the very delayed onset of the significant events in gonadogenesis in the sea lamprey, which in turn are related to the possession of a very high fecundity (Hardisty 1971). Another relevant feature is that, compared with other species, *P. marinus* appears generally to spend a longer time accumulating lipid at the end of larval life.

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ABAKUMOV, V. A. 1960. Systematics and ecology of the Far Eastern Brook lamprey from the Amur River Basin. Vopr. Ikhtiol. 15: 43–54.

ABOU-SEEDO, F. S., AND I. C. POTTER. 1979. The estuarine phase in the spawning run of the River lamprey (*Lampetra fluviatilis*). J. Zool. (London) 188: 5–25.

ÁLVAREZ DEL VILLAR, J. 1966. Ictiologia michoacana, IV. Contribucíon al conocimiento biológico y sistemático de las lampreas de Jacona, Mich., México. An. Esc. Nac. Cienc. Biol. Mexico City 13: 107–144.

APPLEGATE, V. C. 1950. Natural history of the sea lamprey, *Petromyzon marinus*, in Michigan. Spec. Sci. Rep. U.S. Wildl. Serv. Fish. 55: 1–237.

APPLEGATE, V. C., AND C. L. BRYNILDSON. 1952. Downstream movement of recently transformed sea lampreys, *Petromyzon marinus*, in the Carp Lake River, Michigan. Trans. Am. Fish. Soc. 81: 275–290.

APPLEGATE, V. C., AND M. L. H. THOMAS. 1965. Sex ratios and sexual dimorphism among recently transformed sea lampreys, *Petromyzon marinus* Linnaeus. J. Fish. Res. Board Can. 22: 695–711.

BAGENALL, T. B. 1974. Ageing of fish. Unwin, Old Woking, UK.

BAXTER, E. W. 1957. Lamprey distribution in streams and rivers. Nature (London) 180: 1145.

BEAMISH, F. W. H., AND I. C. POTTER. 1972. Timing of changes in the blood, morphology and behavior of *Petromyzon marinus* during metamorphosis. J. Fish. Res. Board Can. 29: 1277–1282.

1975. The biology of the anadromous sea lamprey (*Petromyzon marinus*) in New Brunswick. J. Zool. (London) 177: 57–72.

BEAMISH, F. W. H., I. C. POTTER, AND E. THOMAS. 1979. Proximate composition of the adult anadromous sea lamprey, *Petromyzon marinus* L., in relation to feeding, migration and reproduction. J. Anim. Ecol. 48: 1–19.

BEAMISH, F. W. H., P. D. STRACHAN, AND E. THOMAS. 1978. Osmotic and ionic performance of the anadromous sea lamprey, *Petromyzon marinus*. Comp. Biochem. Physiol. 60A: 435–443.

BIRD, D. J., AND I. C. POTTER. 1979a. Metamorphosis in the paired species of lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). 1. A description of the timing and stages. J. Linn. Soc. London Zool. 65: 127–143.

1979b. Metamorphosis in the paired species of lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). 2. Quantitative data for body proportions, weights, lengths and sex ratios. J. Linn. Soc. London Zool. 65: 145–160.

CHURCHILL, W. S. 1947. The brook lamprey in the Brule River. Trans. Wisconsin Acad. Sci. Arts Lett. 37: 337–346.

DAMAS, H. 1950. La ponte en aquarium des lamproies fluviatiles et de planer. Ann. Soc. R. Zool. Belg. 81: 151–162.

DEAN, B., AND F. B. SUMNER. 1898. Notes on the spawning habits of the brook lamprey (*Petromyzon wilderi*). Trans. New York Acad. Sci. 16: 321–324.

DENDY, J. S., AND D. C. SCOTT. 1953. Distribution, life history and morphological variations of the southern brook lamprey, *Ichthyomyzon gagei*. Copeia 1953: 152–162.

DINES, R. A. 1973. Changes in the morphology, lipid and water of metamorphosing *Lampetra planeri* (Bloch), together with observations on the larval velum and pharynx. Ph.D. thesis, Univ. Bath, Bath, UK.

EDDY, J. M. P. 1969. Metamorphosis and the pineal complex in the brook lamprey, *Lampetra planeri*. J. Endocrinol. 44: 451–452.

1972. The pineal complex, p. 91–103. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2. Academic Press, London.

EGLITE, R. 1958. The biology of the river lamprey in the Latvian SSR. Gidrobiol. Issled. Tallinn 1: 238–269.

ENEQUIST, P. 1937. Das Bachneunauge als ökologische Modification des Flusseneunauges. Über die Fluss — und Bachneunaugen Schwedens. Ark. Zool. 29: 1–22.

GAGE, S. H. 1928. The lampreys of New York State — life history and economics. Biological survey of the Oswega River System. NY State Conserv. Dep. Ann. Rep. 17: 158–191.

GRITSENKO, O. F. 1968. (On the question of an ecological parallelism between lampreys and salmon). Izv. Tikhookean. Nauchno -Issled. Inst. Rybn. Khoz. Okeanogr. 65: 157–169. (In Russian) (K voprusu ob Ekologicheskoh parallizme mezhdu minogami i lesosyami).

HARDISTY, M. W. 1944. The life history and growth of the brook lamprey (*Lampetra planeri*). J. Anim. Ecol. 13: 110–122.

1956. Some aspects of osmotic regulation in lampreys. J. Exp. Biol. 33: 431–447.

1961a. Studies on an isolated spawning population of the brook lamprey (*Lampetra planeri*). J. Anim. Ecol. 30: 339–355.

1961b. The growth of larval lampreys. J. Anim. Ecol. 30: 357–371.

1965. Sex differentiation and gonadogenesis in lampreys. II. The ammocoete gonads of the landlocked sea lamprey, *Petromyzon marinus* L. J. Zool. (London) 146: 346–387.

1969. Information on the growth of the ammocoete larva of the anadromous sea lamprey *Petromyzon marinus* in British rivers. J. Zool. (London). 159: 139–144.

1971. Gonadogenesis, sex differentiation and gametogenesis, p. 295–359. *In* M. W. Hardisty and I. C. Potter [ed.]. The biology of lampreys. Vol. 1. Academic Press, London.

HARDISTY, M. W., AND R. J. HUGGINS. 1970. Larval growth in the river lamprey, *Lampetra fluviatilis*. J. Zool. (London) 161: 549–559.

HARDISTY, M. W., AND I. C. POTTER. 1971a. The behaviour, ecology and growth of larval lampreys, p. 85–125. *In* M. W. Hardisty and I. C. Potter [ed.]. The biology of lampreys, Vol. I. Academic Press, London.

1971b. The general biology of adult lampreys, p. 127–206. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. I. Academic Press, London.

HARDISTY, M. W., I. C. POTTER, AND R. STURGE. 1970. A comparison of the metamorphosing and macrophthalmia stages of the lampreys, *Lampetra fluviatilis* and *L. planeri*. J. Zool. (London) 162: 383–400.

HEARD, W. R. 1966. Observations on lampreys in the Naknek River System of Southwest Alaska. Copeia 1966: 333–339.

HOAR, W. S. 1976. Smolt transformation: evolution, behaviour and physiology. J. Fish. Res. Board Can. 33: 1234–1252.

HODGES, J. W. 1972. Downstream migration of recently transformed sea lampreys before and after treatment of a Lake Michigan tributary with a lampricide. J. Fish. Res. Board Can. 29: 1237–1240.

HUBBS, C. L. 1971. *Lampetra* (*Entosphenus*) *lethophaga*, new species, the nonparasitic derivative of the Pacific Lamprey. Trans. San Diego Soc. Nat. Hist. 16: 125–164.

IVANOVA-BERG, M. M. 1931. Uber die Lebensdauer der Larve von *Lampetra planeri* aus den Gebiete des Finnischen Busens. Zool. Anz. 96: 330–334.

JONES, J. W. 1959. The salmon. Collins, London.

LARK, J. G. I. 1973. An early record of the sea lamprey (*Petromyzon marinus*) from Lake Ontario. J. Fish. Res. Board Can. 30: 131–133.

LEACH, W. J. 1940. Occurrence and life history of the northern brook lamprey, *Ichthyomyzon fossor*, in Indiana. Copeia 1940: 21–34.

1951. The hypophysis of lampreys in relation to the nasal apparatus. J. Morphol. 90: 217–246.

LÉGER, M. L. 1920. Jeunes stades d'eau douce et biologie de la lamproie marine. C.R. Acad. Sci. 179: 251–255.

LENNON, R. E. 1954. Feeding mechanism of the sea lamprey and its effect on host fishes. Fish. Bull. Fish. Wildl. Serv. U.S. 56: 247–293.

LOHNISKY, K. 1966. The spawning behaviour of the brook lamprey, *Lampetra planeri* (Bloch, 1784). Vest. Cesk. Spol. Zool. 30: 289–307.

LOMAN, J. C. C. 1912. Uber die Naturgeschichte des Bachneunauges *Lampetra planeri* (Bloch). Zool. Jahrb. (Suppl.) 15: 243–270.

LONG, C. W. 1968. Diel movement and vertical distribution of juvenile anadromous fish in turbine intakes. Fish. Bull. U.S. 66: 599–609.

LOWE, D. R., F. W. H. BEAMISH, AND I. C. POTTER. 1973. Changes in the proximate body composition of *Petromyzon marinus* (L.) during larval life and metamorphosis. J. Fish. Biol. 5: 673–682.

LUBOSCH, W. 1903. Ueber die Geschlechtsdifferenzierung bei Ammocoetes. Verh. Anat. Ges. 17: 66–74.

MALMQUIST, B. 1978. Population structure and biometry of *Lampetra planeri* (Bloch) from three different watersheds in south Sweden. Arch. Hydrobiol. 84: 65–86.

1980. Habitat selection of larval brook lampreys (*Lampetra planeri*, Bloch) in a south Swedish stream. Oecologia 45: 35–38.

MANION, P. J. 1968. Production of sea lamprey larvae from nests in two Lake Superior streams. Trans. Am. Fish. Soc. 97: 484–486.

1969. Evaluation of lamprey larvicides in the Big Garlic River and Saux Head Lake. J. Fish. Res. Board Can. 26: 3077–3082.

MANION, P. J., AND A. L. MCLAIN. 1971. Biology of larval sea lampreys (*Petromyzon marinus*) of the 1960 year class, isolated in the Big Garlic River, Michigan, 1960–65. Great Lakes Fish. Comm. Tech. Rep. 16: 35 p.

MANION, P. J., AND B. R. SMITH. 1978. Biology of larval and metamorphosing sea lampreys, *Petromyzon marinus*, of the 1960 year class in the Big Garlic River, Michigan Part II, 1966–72. Great Lakes Fish. Comm. Tech. Rep. 30: 35 p.

MANION, P. J., AND T. M. STAUFFER. 1970. Metamorphosis of the landlocked sea lamprey, *Petromyzon marinus*. J. Fish. Res. Board Can. 27: 1735–1746.

MASKELL, F. G. 1929. On the New Zealand lamprey, *Geotria australis* Gray. 1. Biology and life history. Trans. N.Z. Inst. 60: 167–201.

MCCAULEY, R. W. 1963. Lethal temperatures of the developmental stages of the sea lamprey, *Petromyzon marinus* L. J. Fish. Res. Board Can. 20: 483–490.

MOORE, J. W., AND I. C. POTTER. 1976. Aspects of feeding and lipid deposition and utilization in the lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). J. Anim. Ecol. 45: 699–712.

MORRIS, R. 1972. Osmoregulation, p. 193–239. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2. Academic Press, London.

NEAVE, F. 1955. Notes on the seaward migration of pink and chum salmon fry. J. Fish. Res. Board Can. 12: 369–374.

O'BOYLE, R. N., AND F. W. H. BEAMISH. 1977. Growth and intermediary metabolism of larval and metamorphosing stages of the landlocked sea lamprey, *Petromyzon marinus* L. Environ. Biol. Fish. 2: 103–120.

OKKELBERG, P. 1922. Notes on the life history of the brook lamprey *Ichthyomyzon unicolor*. Occas. Pap. Mus. Zool. Univ. Mich. 125: 14 p.

OOI, E. C., AND J. H. YOUSON. 1976. Growth of the opisthonephric kidney during larval life in the anadromous sea lamprey, *Petromyzon marinus* L. Can. J. Zool. 54: 1449–1458.

PERLMUTTER, A. 1951. An aquarium experiment on the American eel as a predator on larval lampreys. Copeia 1951: 173–174.

PIAVIS, G. W. 1971. Embryology, p. 361–400. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. I. Academic Press, London.

POTTER, I. C. 1968. *Mordacia praecox* n. sp. a nonparasitic lamprey (Petromyzonidae), from New South Wales, Australia. Proc. Linn. Soc. N.S.W. 92: 254-261.

1970. The life cycles and ecology of Australian lampreys of the genus *Mordacia*. J. Zool. (London) 161: 487–511.

1980. The Petromyzoniformes with particular reference to paired species. Can. J. Fish. Aquat. Sci. 37: 1595–1615.

POTTER, I. C., AND J. R. BAILEY. 1972. The life cycle of the

Tennessee brook lamprey *Ichthyomyzon hubbsi* Raney. Copeia 1972: 470–476.

POTTER, I. C., AND F. W. H. BEAMISH. 1977. The freshwater biology of adult anadromous sea lampreys *Petromyzon marinus*. J. Zool. (London) 181: 113–130.

POTTER, I. C., F. W. H. BEAMISH, AND B. G. H. JOHNSON. 1974. Sex ratios and lengths of adult sea lampreys (*Petromyzon marinus*) from a Lake Ontario tributary. J. Fish. Res. Board Can. 31: 122–124.

POTTER, I. C., AND I. D. BROWN. 1974. Changes in haemoglobin electropherograms during the life cycle of two closely related lampreys. Comp. Biochem. Physiol. 51B: 517–519.

POTTER, I. C., B. J. HILL, AND S. GENTLEMAN. 1970. Survival and behaviour of ammocoetes at low oxygen tensions. J. Exp. Biol. 53: 59–73.

POTTER, I. C., R. W. HILLIARD, AND D. J. BIRD. 1980. Metamorphosis in the Southern Hemisphere lamprey, *Geotria australis* Gray. J. Zool. (London). 190: 405–430.

POTTER, I. C., AND R. J. HUGGINS. 1973. Observations on the morphology, behaviour and salinity tolerance of downstream migrating river lampreys (*Lampetra fluviatilis*). J. Zool. (London) 169: 365–379.

POTTER, I. C., W. J. R. LANZING, AND R. STRAHAN. 1968. Morphometric and meristic studies on populations of Australian lampreys of the genus *Mordacia*. J. Linn. Soc. London Zool. 47: 533–546.

POTTER, I. C., G. M. WRIGHT, AND J. H. YOUSON. 1978. Metamorphosis in the anadromous sea lamprey, *Petromyzon marinus* L. Can. J. Zool. 56: 561–570.

PURVIS, H. A. 1970. Growth, age at metamorphosis and sex ratio of northern brook lamprey in a tributary of southern Lake Superior. Copeia 1970: 326–332.

1979. Variations in growth, age at transformation, and sex ratio of sea lampreys reestablished in chemically treated tributaries of the upper Great Lakes. Great Lakes Fish. Comm. Tech. Rep. 35: 36 p.

1980. Effects of temperature on metamorphosis and the age and length at metamorphosis in sea lamprey (*Petromyzon marinus*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1827–1834.

RANDALL, D. J. 1972. Respiration, p. 287–306. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys Vol. 2. Academic Press, London.

REIGHARD, J. 1903. An experimental study of the spawning behavior of *Lampetra wilderi*. Science, N.Y. 17: 529.

REYNOLDS, W. W., AND M. E. CASTERLIN. 1978. Behavioural thermoregulation by ammocoete larvae of the sea lamprey (*Petromyzon marinus*) in an electronic shuttlebox. Hydrobiologia 61: 145–147.

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

SCHROLL, F. 1959. Zur Ernährungsbiologie der steirischen Ammocöten *Lampetra planeri* (Bloch) und *Eudontomyzon danfordi* (Regan). Int. Rev. Gesamten Hydrobiol. 44: 395–429.

SCHULTZ, L. P. 1930. The life history of *Lampetra planeri* Bloch, with a statistical analysis of the rate of growth of the larvae from western Washington. Occas. Pap. Mus. Zool. Univ. Mich. 221: 1–35.

SMITH, B. R. 1971. Sea lampreys in the Great Lakes of North America, p. 207–247. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. I. Academic Press, London.

SMITH, B. R., AND A. L. MCLAIN. 1962. Estimation of the brook and sea lamprey ammocoete populations of three streams. Great Lakes Fish. Comm. Tech. Rep. 4: 18 p.

SOLOMON, D. J. 1978. Some observations on salmon smolt migration in a chalkstream. J. Fish. Biol. 12: 571–574.

STERBA, G. 1962. Die Neunaugen (Petromyzonidae), p. 263–352. *In* R. Demolt, H. N. Maier et al. [ed.] Handbuch der Binnenfischerei Mitteleuropas, Vol. III. E. Schweizerbart, Stuttgart.

THOMAS, J. D. 1962. The food and growth of brown trout (*Salmo trutta* L.) and its feeding relationship with the salmon parr (*Salmo salar* L.) and the eel (*Anguilla anguilla* L.) in the River Teify, West Wales. J. Anim. Ecol. 31: 175–205.

THOMAS, M. L. H. 1962. Observations on the ecology of ammocoetes of *Petromyzon marinus* L. and *Entosphenus lamottei* (Le Sueur) in the Great Lakes watershed. M.Sc. thesis. Univ. Toronto, Toronto, Ont.

TORBLAA, R. L., AND R. W. WESTMAN. 1980. Ecological impacts of lampricide treatments on sea lamprey (*Petromyzon marinus*) ammocoetes and metamorphosed individuals. Can. J. Fish. Aquat. Sci. 37: 1835–1850.

VLADYKOV, V. D. 1949. Quebec lampreys (Petromyzonidae). 1. List of species and their economical importance. Contrib. Dep. Pech. Que. 26: 1–67.

WAGNER, W. C., AND T. M. STAUFFER. 1962. Sea lamprey larvae in lentic environments. Trans. Am. Fish. Soc. 91: 384–387.

WIGLEY, R. L. 1959. Life history of the sea lamprey of Cayuga Lake, New York. U.S. Fish. Wildl. Serv. Fish. Bull. 59: 559–617.

YOUNG, R. T., AND L. J. COLE. 1900. On the nesting habits of the brook lamprey *Lampetra wilderi*. Am. Nat. 34: 617–620.

YOUSON, J. H., J. LEE, AND I. C. POTTER. 1979. The distribution of fat in larval, metamorphosing, and young adult anadromous sea lampreys, *Petromyzon marinus* L. Can. J. Zool. 57: 237–246.

YOUSON, J. H., AND I. C. POTTER. 1979. A description of the stages in the metamorphosis of the anadromous sea lamprey, *Petromyzon marinus* L. Can. J. Zool. 57: 1808–1817.

YOUSON, J. H., G. M. WRIGHT, AND E. C. OOI. 1977. The timing of changes in several internal organs during metamorphosis of anadromous larval lamprey *Petromyzon marinus* L. Can. J. Zool. 55: 469–473.

ZANANDREA, G. 1951. Rilievi e confronti biometrici e biologici sul *Petromyzon* (*Lampetra*) *planeri*, Bloch, nelle acque della Marca Trevigiana. Boll. Pesca Piscic. Idrobiol. 6(1): 1–28.

1961. Studies on European lampreys. Evolution 15: 523–534.

Feeding of Larval Lamprey[1]

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The feeding mucus in larval lamprey is produced by the lateral walls of the pharynx and by glandular goblet cells on gill filaments. The mucous complex has 14 lateral branches which move inward to the middle of the pharynx, where they are collected and directed back to the esophagus. Mucus, which is carried by intrapharyngeal ciliary tracts and water currents, fills virtually every space in the pharynx, resulting in high (75%) entrapment efficiency. Based on indirect calculations, algae accounted for only 0.14–1.5% of the gut contents in larvae of European brook lamprey (*Lampetra planeri*). Although the bacterial film associated with algae, detritus, and sand grains may be an energy source for ammocoetes, suspended bacteria cannot support growth in laboratory experiments. Selective feeding on different species of algae is common among lampreys and is based on three factors: (1) susceptibility to capture in the feeding–respiratory flow differs among particles, (2) filtration of long filaments by the oral cirri, and (3) selective agglutination at the mucous filter. *Fragilaria*, *Cocconeis*, and *Oscillatoria* species are present in relatively low numbers in the gut whereas *Navicula* species are ingested with greater frequency than they occur in the environment. The size distribution of ingested particles is, in general, independent of the size of the ammocoete. Feeding rate depends on temperature and to a lesser extent, food density. In the laboratory, ammocoetes digest and assimilate only 30–40% of the protein, lipid, and carbohydrate (excluding cellulose) and 6–7% of the cellulose in their food. Therefore, larvae of many species pass large quantities of undigested algae and other food through their guts, particularly at low temperatures.

Key words: algae, ammocoetes, assimilation efficiency, bacteria, detritus, feeding, lamprey, mucous complex

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Le mucus alimentaire de la lamproie larvaire est produit par les parois latérales du pharynx et par des cellules caliciformes glandulaires situées sur les filaments branchiaux. Le complexe muqueux comprend 14 branches latérales qui se déplacent à l'intérieur vers le milieu du pharynx où elles sont collectées et ramenées vers l'oesophage. Le mucus, transporté par des faisceaux ciliaires intrapharyngiens et des courants d'eau, remplit pratiquement tout le pharynx avec, comme résultat, une grande efficacité (75%) d'emprisonnement. Des calculs indirects indiquent que le contenu du tractus digestif de larves de *Lampetra planeri* ne comprenait que 0,14–1,5% d'algues. Bien que la pellicule bactérienne associée aux algues, aux détritus et aux grains de sable puisse être une source énergétique pour les ammocètes, les bactéries en suspension ne peuvent supporter la croissance dans des expériences de laboratoire. On observe communément chez les lamproies une alimentation sélective à même trois espèces différentes d'algues, fondée sur 3 facteurs : (1) la susceptibilité à la capture dans le courant alimentaire-respiratoire diffère d'une particule à l'autre, (2) la filtration des longs filaments par les cirri buccaux et (3) l'agglutination sélective au filtre muqueux. Les espèces de *Fragilaria*, *Cocconeis* et *Oscillatoria* se rencontrent en nombres relativement faibles, alors que celles de *Navicula* sont absorbées à une fréquence supérieure à celle où elles se trouvent dans le milieu. La répartition des tailles des particules absorbées est en général indépendante de la taille des ammocètes. Le taux d'alimentation dépend de la température et, à un degré moindre, de la densité des aliments. En laboratoire, les ammocètes ne digèrent et assimilent que 30–40% des protéines, lipides et hydro-

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carbures (cellulose non comprise) et 6–7% de la cellulose contenus dans la nourriture. Les larves de plusieurs espèces éliminent donc par leur tractus digestif de grandes quantités d'algues et autres aliments non digérés, en particulier aux basses températures.

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LARVAL lampreys are filter feeders, which usually inhabit burrows in the soft sediments of streams. Potential food items are carried by the unidirectional respiratory current through a ring of coarse oral cirri into the pharynx (Randall 1971; Sterba 1961, 1962). The meshwork of cirri acts as a sieve, preventing large particles from entering the pharyngeal chamber. These particles are enmeshed in mucus on the cirri and are periodically expelled through a "coughing" action (Applegate 1950). The purpose of this paper is to review the literature on the feeding biology of larval lampreys; included are a description of the feeding mechanism, source and composition of food, selective feeding, and feeding rates, entrapment, and digestion efficiency.

The Feeding Mechanism

It was suggested in previous studies (Kieckebusch 1928; Newth 1930; Balabai 1950; Young 1950; Sterba 1961, 1962) that suspended food particles are trapped by a mucous cord (the food cord) extending the length of the central portion of the pharynx. The mucus was thought to be secreted by the subpharyngeal gland or endostyle. However, Mallatt (1980) showed that gladular goblet cells, occupying the lateral portion of each gill filament, and the lateral walls of the pharynx, produce the feeding mucus. The mucus is secreted in large quantities and forms an intricate complex which fills virtually every space within the pharynx. The mucous complex has 14 similar lateral branches (one per gill pouch) which move inward to the central part of the pharynx. Here, they are collected into a longitudinal band (the food cord of previous authors) and directed back to the esophagus. The mucus is directed primarily by intrapharyngeal ciliary tracts, but also by water currents. Particle entrapment occurs throughout the mucous complex, although the largest particles (100 to 300 μm in diameter) are trapped most centrally. Particles and mucus aggregate as they move inward across the gill pouches. Thus, the mucous complex serves the multiple functions of trapping, aggregating, and transporting food particles. This manner of feeding seems to be common to ammocoetes of all sizes and genera.

Since the entrapping mucus originates in the lateral part of the pharynx, the medially situated endostyle is evidently not its source. The function of this gland is to add secretions such as digestive enzymes and iodoproteins (Clements-Merlini 1960; Hoheisel 1969) to the highly condensed central portion of the mucous complex.

Source of Food

Because ammocoetes are filter feeders, much of their food is suspended material. Creaser and Hann (1929) indicated that the food was drawn from the water immediately above the substrate where microorganisms are particularly dense. Although subsequent studies (Wigley 1959; Manion 1967) have confirmed that ammocoetes feed primarily on suspended material, the constant shifting of sediments and movement of larvae indicate that benthic organisms are consumed to a varying degree. Furthermore, since the burrows at the substrate surface are sometimes closed off, lamprey cannot consume suspended food at that time. Thus, food may be drawn from the water or a combination of the water and sediments, depending on environmental conditions and activity of the ammocoetes.

Composition of Food

There is little quantitative information on the relative importance of various foods in the nutrition of larval lampreys. On the basis of cell counts, Creaser and Hann (1929) concluded that diatoms and desmids were frequently eaten by American brook lamprey (*Lampetra lamottenii*) (*Entosphenus appendix* of Creaser and Hann) during the summer. Although ciliated protozoans were also believed to be ingested, these could not be identified because of their rapid digestion. Subsequent studies, using semiquantitative methods such as cell counts, and determinations of surface areas have reemphasized that algae, particularly diatoms, are found in ammocoetes (Sterba 1953; Manion 1967; Schroll 1959; Alvarez del Villar 1966; Potter et al. 1975). Predominant taxa in the guts of lampreys usually include *Navicula*, *Cymbella*, *Gomphonema*, *Nitzschia*, *Pinnularia*, and *Achnanthes* species. These forms are also common in the water and sediments of temperate zone streams (Hynes 1972).

Detritus is frequently reported in the gut contents of all species of lampreys, although its relative abundance may vary with season and locality (Hardisty and Potter 1971). For example, Schroll (1959) found that the quantity of ingested detritus (<65% of gut contents) in European brook lamprey (*Lampetra planeri*) was greatest in the winter when algal densities were low in the environment. Although Sterba (1962) recorded significant amounts of ingested detritus in *L. planeri* during the summer, this material was rare in the guts of the Australian lamprey *Mordacia mordax* collected from a stream in Australia (Potter et al.

TABLE 1. Percentage contribution of algae to the gut contents of several species of herbivores. Data expressed in terms of weight,[1] volume,[2] or caloric content.[3]

Species	Algal abundance (%)	Habitat	Reference
Lamprey			
Lampetra planeri[1]	0.14	Woodland stream (England)	This study
Insects			
Ephemeroptera (several species)[3]	3.5–92.1	Woodland streams (Pennsylvania, Kentucky)	Cummins (1973)
Plecoptera (several species)[2]	1–45	Woodland streams (Wisconsin)	Shapas and Hilsenhoff (1976)
Oligochaetes			
Lumbriculus variegatus[2]	70–85	Great Slave Lake	Moore (1978)
Mollusks			
Lymnaea auricularia[1]	85	Lake Zurich	Knecht and Walter (1977)

1975). Based on laboratory experiments, Moore and Potter (1976a) showed that, at 15°C, larvae of *L. planeri* gained $\sim$2% in wet body weight when fed detritus for 60 d. Since the detritus used in their studies was not presterilized, some growth may have been attributable to the associated bacterial film. Detritus, a poor energy source, is very high (90–95%) in cellulose, lignin, and ash (Calow 1973; Monk 1976).

Because of the difficulties involved in separating microscopic particles in the gut contents, gravimetric estimates of the relative abundances of algae and detritus have not been made for ammocoetes. Therefore, current estimates of the quantities of ingested algae and detritus are probably subject to error and should be considered tentative. Although biochemical techniques of estimating the biomass of ingested microorganisms are available (Moriarty 1976, 1977), they have not been used to estimate good consumption ammocoetes.

To obtain a better (albeit indirect) estimate of the relative abundance of algae and detritus in *L. planeri* inhabiting Highland Water in southern England (Moore and Potter 1976b), the maximum volume of ingested algae ($9 \times 10^6\ \mu m^3$) reported for a 1.0-g ammocoete can be transformed into an estimate of biomass, assuming a specific gravity of 1. This transformation, based on direct microscopic measurements of the length, width, and depth of algae to estimate volume, is frequently used in phycological studies. Therefore, the wet weight of ingested algae in *L. planeri* was 0.009 mg per animal, which is equivalent to $\sim$0.006 mg in terms of dry weight. Since the maximum dry weight of gut contents was 4.3 mg, algae comprised only 0.14% of dry gut contents. For the flora to constitute 50% of the ingested material, $3.2 \times 10^9\ \mu m^3$ would have to be found in a 1.0-g ammocoete, which is approximately equivalent to 10×16^6 cells per animal. Such large numbers have not been found in any species. In most cases the number of ingested cells is $<0.5 \times 10^6$ per animal (Potter et al. 1975). In a eutrophic agricultural stream in southern England, the microflora accounted for 1.5% by volume of the gut contents of *L. planeri* (Moore and Potter 1976b). Based on these results, larvae of *L. planeri* contain far less algae in their guts than other herbivorous species (Table 1). Since microphagous feeders, including ammocoetes, pass mixtures of different food items through their gut at the same rate (Moore and Beamish 1973), it is not necessary to include a time factor in the analysis of the preceding data.

Although there are no estimates of the importance of attached bacteria and fungi in the feeding of larval lampreys, such nutriment supports the growth and reproduction of many other herbivorous species. Smyly and Collins (1975) showed that the cladoceran *Ceriodaphnia quadrangula* could be maintained solely on the bacteria associated with the alga *Scenedesmus*. Their studies also demonstrated that, while algae were frequently ingested, they played no part in the nutrition of *C. quadrangula*. Similarly Brinkhurst et al. (1972) considered that attached bacteria were the only significant food source for oligochaetes whereas Moriarty (1976) reported that 30% of the carbon in the guts of the prawn *Metapenaeus bennettae* was of bacterial origin and that algae were unimportant in the food of most specimens. Based on these comparisons and the small contribution of algae to the gut contents of *L. planeri*, the bacteria and fungi attached to detritus, sand grains, and algae are probably more important to the nutrition of larval lampreys than has been previously thought.

Planktonic bacteria are a potential food source, which may partially govern the distribution of larvae. Hardisty and Potter (1971), for example, found relatively high densities of ammocoetes in the vicinity of decaying animal carcasses. However, in experimental tanks with a slight ($<5\ cm \cdot s^{-1}$) current, *L. planeri* gained only 0.5% in wet weight when fed *Escherichia coli* at a concentration of 1×10^8 cells$\cdot$mL^{-1} for 60 d (Moore and Potter 1976a). Such densities are extremely high and would not be encountered in a lamprey stream. The preceding experiments also demonstrated that lamprey lost weight when fed at 1×10^6 and 1×10^5 bacteria$\cdot$mL^{-1}. In contrast, Freeden (1964) reared *Simulium* in the laboratory on nothing but bacteria.

Protozoans, nematodes, and rotifers are occasionally found among the gut contents of lamprey. Since the total number of organisms in the gut is generally small, often <10 per animal, they cannot be an important food source in most streams (Moore and Beamish 1973; Potter et al. 1975). In addition, nematodes and rotifers often show little indication of digestion in *P. marinus* and *L. lamottenii* (Moore and Beamish 1973).

Selective Feeding

Although the importance of the various dietary items of lamprey is not known, there have been some examples of selective feeding on different species of algae. Manion (1967) found that the diatom *Navicula* made up 32.9% of the flora in sea lamprey (*Petromyzon marinus*) larvae measuring 70–72 mm in length, while corresponding values for 33–35 mm specimens and in the water were 19.1 and 11.5%, respectively. This same species rarely consumed algae attached to sand grains (*Cocconeis* and *Amphora* species) and very long diatoms such as *Diatoma* and *Oscillatoria*, even though these forms were common on the sediments and in the water (Moore and Beamish 1973).

Because potential food items are drawn towards the larvae in a unidirectional respiratory current, selective feeding (Fig. 1) depends on the susceptibility of algae to capture in the respiratory current. This accounts for the scarcity in *P. marinus* of large algae (Fig. 1) and species attached to sand grains (Moore and Beamish 1973). Once inside the oral hood, microscopic algae probably have little difficulty in passing through the oral cirri. The cirri are coarse and, although they afford a mechanical limitation based on size, their main function is to limit large detrital particles and algal filaments from entering the pharynx. Manion (1967) demonstrated that filaments of *Fragilaria* species were rarely consumed by *P. marinus*, presumably due to filtration at the oral cirri. Similarly, Moore and Beamish (1973) found that 1-mm-long filaments of *D. vulgare* and *O. limosa* and *O. tenuis* could not pass through the cirri.

Once inside the pharyngeal chamber, the primary site of selection is the mucous complex. Schroll (1957, 1959) demonstrated that diatoms, sand grains, and carbon readily adhered to the mucus in larvae of *L. planeri* and Hungarian lamprey (*Eudontomyzon danfordi*), whereas certain species of protozoans and parts of oligochaetes were not taken up by the filter. In addition, Potter et al. (1975) suggested that the spines on *Scenedesmus* readily embedded in the mucus of *Mordacia* and consequently this alga appeared in disproportionately large numbers in the gut.

Algae within the diatom genus *Navicula* usually appear more frequently in the gut contents than in the environment (Manion 1967; Moore and Beamish 1973). Although this may result from selective agglutination (Schroll 1959), the exclusion of other algae from the gut due to size selection implies that all other species must be ingested with greater frequency than their abundance in the environment. Therefore, the apparent selection for *Navicula* is the result of exclusion of other genera based on size. Similarly, *Scenedesmus* species represented 31.2% by numbers of the gut contents of *Mordacia mordax* and only 0.9% of the flora in the environment (Potter et al. 1975). This suggested that there was a selective mechanism preventing the consumption of all species of diatoms. However, the abundance of ingested diatoms in the absence of *Scenedesmus* indicates that the relative proportion of diatoms in the gut was similar to that in the environment.

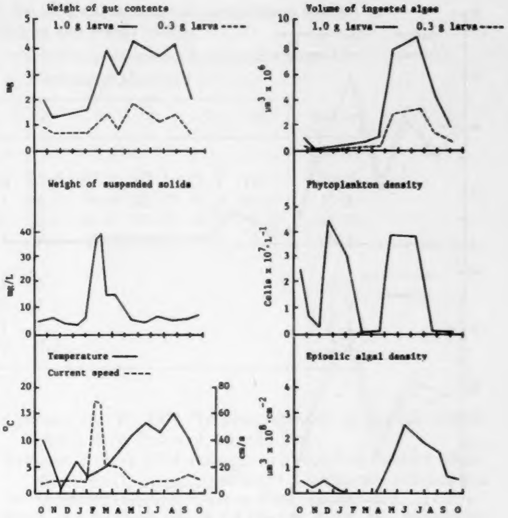

FIG. 1. Length distribution of algae in the guts of sea lampreys of different length and in the water and sediments of Shelter Valley Creek (Ont.) during September 1971. (Data recalculated from Moore and Beamish 1973.)

Although size selection limits the consumption of large particles (>340 μm), algae which are 5–340 μm were particularly common in both large and small ammocoetes and were also prevalent in the environment. Furthermore, taxa of 21–30 and 51–70 μm were also less abundant in the environment. The largest algae (*Nitzschia sigmoidea*) found in the gut of larvae >10.5 cm averaged 313 μm in length whereas in specimens of less than 3.5 cm, the corresponding average was 340 μm. Based on these data, we conclude that the size distribution of particles ingested by ammocoetes of <3.5 cm is similar to that recorded for specimens >10.5 cm, and that there is no selection based on size within the 5- to 340-μm range.

Since the main species of algae in streams measure

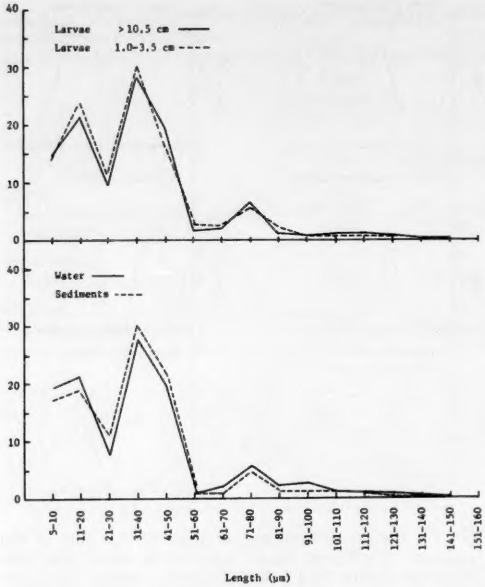

FIG. 2. Seasonal changes in the dry weight of gut contents and the number of ingested cells in *Lampetra planeri*, and in environmental conditions in Highland Water (southern England). (Data from Moore and Potter 1976b.)

>5 µm at all stages of their life cycle, there have been no examples of selection by lampreys for small algae. Since particle entrapment involves capture by impaction on mucus rathar than filtration by fixed pore size, there is no priori reason why there should be an abrupt lower size limit to particles ammocoetes can trap (see Rubenstein and Koehl 1977). However, most of the smallest particles, such as suspended bacteria, probably pass out of the pharynx into the water which would explain the inability of larvae to gain weight on this food source. Overall, therefore, most examples of selective feeding are based on particle size.

Feeding Rates, Entrapment, and Digestion Efficiencies

There is a seasonal variation in the feeding rate of ammocoetes in northern temperate zone streams. In Highland Water in southern England, *L. planeri* began feeding intensively in March as the water temperature increased from 5 to 12°C (Moore and Potter 1976b) (Fig. 2). Since the spring bloom of algae occurred about 2 mo after this increase, the availability of algae was not involved in the initiation of increased feeding activity. There was also an inverse relationship between the quantity of material suspended in the water and the weight of the gut contents. This implied that the total amount of food potentially available in the environment had little influence on the quantity of ingested matter. During the summer in Highland Water, the quantity of ingested matter remained relatively constant and declined in October at a temperature of 10°C. Therefore the intensity of feeding was less during the fall than in the spring, despite the similarity in water temperatures. It is not known if there is an optimal temperature for food intake in lampreys.

Like other suspension feeders (Lam and Frost 1976), ammocoetes regulate food intake according to availability. For example, Mallatt (1979), found that within the range 0.5 to 85 mg dry yeast·L^{-1} (*Saccharomyces cereviseae*) the flow of water into the pharynx (F) in *P. marinus* increases with yeast concentration (C) according to the formula: $F = 31 + 5.2\,C^{0.3}$ mL·h^{-1}·g^{-1} for a 1.6-g animal at 12.5°C. If C exceeds 85 mg·L^{-1}, however, flow rate decreases presumably because ingested material interferes with normal feeding and respiration The data suggest that, except at high concentrations of food, ammocoetes consume more food as their abundance increases as observed for other suspension feeders. However, while the flow rates of most other suspension feeders begin declining at 2–10 mg·L^{-1}, ammocoete flow rates do not begin to decline until concentrations much higher than this. Mallatt (1979) also demonstrated that flow rate in ammocoetes is much slower, on a unit weight basis, than that of other suspension feeders such as copepods and mollusks This partially reflects the relatively low metabolic rate of lamprey (Hill and Potter 1970) and implies that ammocoetes may need relatively high concentrations of food to sustain growth.

From laboratory experiments, the rate of evacuation of food from the gut of larval sea lampreys required an average of 54 h (range 51–58 h) at 16°C and 70 h (range 60–90 h) at 2.5°, regardless of larval length (Moore and Beamish 1973). There were no differences in the rates at which various species of algae passed through the gut at either temperature.

As in most species of aquatic herbivores (Ivlev 1939; Levanidov 1949; Brown 1961), ammocoetes digest only part of the food in their guts. At 15°C, the larvae of *L. planeri* utilized an average of 39.5% of the lipid in their food, 33.8% of the protein, 35.2% of the carbohydrates (excluding cellulose), and 6.5% of the cellulose (Table 2). The corresponding values for animals maintained at 5°C were 8.0, 3.9, 6.2, and 0.5%. The considerable variation in assimilation efficiency in the different experiments recorded in Table 2 was probably due to the degree of activity of the animals prior to analysis, as noted in other herbivores (Prus 1971; Nilsson 1974). For example, in an active animal (Hardisty and Potter 1971), food passes through the gut much more rapidly than when at rest. Under natural conditions, digestion efficiency is probably relatively high, particularly during low water periods in summer. However, spring floods would likely increase the level of activity in ammocoetes, thereby decreasing digestion efficiency.

TABLE 2. Percentage contribution by weight of the different nutritional components assimilated by larvae of *Lampetra planeri* (data from Moore and Potter 1976a).

Component	Percentage absorbed						
	Expt. 1	2	3	4	5	6	Mean
15°C							
Lipid	5.4	45.5	87.3	62.1	22.7	14.1	39.5
Protein	4.5	44.2	69.9	42.4	31.7	10.3	33.8
Carbohydrate (excluding cellulose)	9.7	38.5	62.4	58.1	9.7	9.7	35.2
Cellulose	6.1	9.5	10.2	3.2	4.5	5.2	6.5
5°C							
Lipid	5.5	10.5					8.0
Protein	1.5	6.3					3.9
Carbohydrate (excluding cellulose)	5.1	7.3					6.2
Cellulose	0.2	0.8					0.5

The inefficient utilization of food by ammcoetes is attributable to the thick cellulose walls that many species of algae possess which are not easily broken down by digestive enzymes. In addition, detritus, potentially the most abundant material in the gut, consists primarily of ash, cellulose, and lignin, which are also not easily broken down. Finally, food embedded in the mucous band may be more resistant to digestion than the material attached to the surface. This poor utilization of food suggests that large quantities of algae must pass thruogh the gut undigested, a view substantiated by work on *P. marinus*, where survival of diatoms was about 45% during the summer and 95% in the winter (Moore and Beamish 1973).

Contrasting with this low efficiency of food utilization is a high efficiency of food entrapment. *Petromyzon marinus* larvae removed an average of 75% of both yeast (diameter = 5 μm) and algal cells (*Chlorella pyrenoidosa*, diameter = 8 μm) from the water passing through the pharynx (Mallatt 1979).

APPLEGATE, V. C. 1980. Natural history of the sea lamprey, *Petromyzon marinus*, in Michigan. Spec. Rep. U.S. Fish. Wildl. Serv. 55: 237 p.

ALVAREZ DEL VILLAR, J. 1966. Ictiologia michoacana, IV. Contribution al Conocimiento Biologico y Sistematico de las Lampreas de Jacona, Mich., Mexico. An. Esc. Nac. Cienc. Biol. Mexico City 13: 107–144.

BALABAI, P. 1950. Observations on the feeding of the ammocoete. Dokl. Akad. Nauk SSSR 72: 341–344. (In Russian)

BRINKHURST, R. O., K. E. CHUA, AND N. K. KAUSHIK. 1972. Interspecific interactions and selective feeding by tubificid oligochaetes. Limnol. Oceanogr. 17: 122–131.

BROWN, D. S. 1961. The food of the larvae of *Chloeon dipterum* L. and *Baetis rhodani* (Pictet) (Insecta, Ephemeroptera). J. Anim. Ecol. 30: 55–75.

CALOW, P. 1973. On the nature and possible utility of epilithic detritus. Hydrobiologia 46: 181–189.

CLEMENTS-MERLINI, M. 1960. The secretory cycle of iodoproteins in ammocoetes. J. Morphol. 106: 337–356.

CREASER, C. W., AND C. S. HANN. 1929. The food of larval lampreys. Pap. Mich. Acad. Sci. Arts Lett. 10: 433–437.

CUMMINS, K. W. 1973. Trophic relations of aquatic insects. Annu. Rev. Entomol. 18: 183–206.

FREEDEN, F. J. H. 1964. Bacteria as a source of food for blackfly larvae (Diptera: Simuliidae) in laboratory cultures and in natural streams. Can. J. Zool. 42: 527–538.

HARDISTY, M. W., AND I. C. POTTER. 1971. The behaviour, ecology and growth of larval lampreys, p. 85–125. *In* M. W. Hardisty and I. C. Potter (ed.) The biology of lampreys. Academic Press, London.

HILL, B. J., AND I. C. POTTER. 1970. Oxygen consumption in ammocoetes of the lamprey *Ichthyomyzon hubbsi* Raney. J. Exp. Biol. 53: 47–57.

HOHEISEL, B. 1969. Untersuchungen zur functionellen Morphologie des Endostyls und der Thyreoiden vom Bachneunauge (*Lampetra planeri* Bloch). I. Untersuchungen am Endostyl. Gegenb. Morphol. Jahrb. 114: 204–237.

HYNES, H. B. N. 1972. The ecology of running waters. Univ. Toronto Press, Toronto, Ont.

IVLEV, V. S. 1939. Transformation of energy by aquatic animals. Coefficient of energy consumption by *Tubifex tubifex* (Oligochaeta). Int. Rev. Gesamten Hydrobiol. Hydrogr. 38: 449–458.

KIECKEBUSCH, H. H. 1928. Beiträge zur Kenntnis des Baues und der Entwicklung der Schilddrüse bei den Neunaugenlarven (*Lampetra fluviatilis* L. and *Lampetra planeri* Bl.) Z. Morphol. Oekol. Tiere 11: 350–354.

KNECHT, V. A., AND J. E. WALTER. 1977. Vergleichende Untersuchung der Diäten von *Lymnaea auricularia* und *L. peregra* (Gastropoda: Basommatophora) im Zurichsee Schweiz. Z. Hydrol. 39: 299–305.

LAM, R. K., AND B. W. FROST. 1976. Model of copepod filtering response to changes in size and concentration of food. Limnol. Oceanogr. 21: 490–500.

LEVANIDOV, U. YA. 1949. Significance of allochthonous material as a food resource in a water body as exemplified by the nutrition of the water louse *Asellus aquaticus* L. Tr. Vses Gidrobiol. Ova. 1: 100–117.

MALLAT, J. 1980. Surface morphology of structures within the pharynx of the larval lamprey *Petromyzon marinus*. J. Morphol. (In press)

1979. The feeding biology of the larval lamprey, *Petromyzon marinus*; mechanisms and regulation of feeding. Ph.D. thesis, Department of Anatomy, Univ. Chicago, Chicago, IL.

MANION, P. J. 1967. Diatoms as food of larval sea lampreys in a small tributary of Northern Lake Michigan. Trans. Am. Fish. Soc. 96: 224–226.

Monk, D. C. 1976. The distribution of cellulose in freshwater invertebrates of different feeding habits. Freshwater Biol. 6: 471–475.

Moore, J. W. 1978. Importance of algae in the diet of the oligochaetes *Lumbriculus variegatus* (Müller) and *Rhyacodrilus sodalis* (Eisen). Oecologia 35: 357–363.

Moore, J. W., and F. W. H. Beamish. 1973. Food of larval sea lamprey (*Petromyzon marinus*) and American brook lamprey (*Lampetra lamottei*). J. Fish. Res. Board Can. 30: 7–15.

Moore, J. W., and I. C. Potter. 1976a. A laboratory study on the feeding of larvae of the brook lamprey *Lampetra planeri* (Bloch). J. Anim. Ecol. 45: 81–90.

1976b. Aspects of feeding and lipid deposition and utilization in the lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). J. Anim. Ecol. 45: 699–712.

Moriarty, D. J. W. 1976. Quantitative studies on bacteria and algae in the food of the mullet *Mugil cephalus* L. and the prawn *Metapenaeus bennettae* (Racek & Dall). J. Exp. Mar. Biol. Ecol. 22: 131–143.

1977. Quantification of carbon, nitrogen and bacterial biomass in the food of some penaeid prawns. Aust. J. Mar. Freshwater Res. 28: 113–118.

Newth, H. G. 1930. The feeding of ammocoetes. Nature 126: 94–95.

Nilsson, L. M. 1974. Energy budget of a laboratory population of *Gammarus pulex* (Amphipoda). Oikos 25: 35–42.

Potter, I. C., D. Cannon, and J. W. Moore. 1975. The ecology of algae in the Moruya River, Australia. Hydrobiologia 47: 415–430.

Prus, T. 1971. The assimilation efficiency of *Asellus aquaticus* L. (Crustacea; Isopoda). Freshwater Biol. 1: 287–305.

Randall, D. J. 1971. Respiration. *In* M. W. Hardisty and I. C. Potter (ed.) The biology of lampreys. Academic Press, London.

Rubenstein, D. I., and M. A. R. Koehl. 1977. The mechanisms of filter feeding: some theoretical considerations. Am. Nat. 111: 981–994.

Schroll, F. 1957. Zur Ernährungsphysiologie der Ammocoetesslarven der Cyclostomen. Zool. Anz. 159: 75–78.

1959. Zur Ernährungsphysiologie der steirischen Ammocöten *Lampetra planeria* (Bloch) and *Eudontomyzon danfordi* (Regan). Int. Rev. Gesamten Hydrobiol. Hydrogr. 44: 395–429.

Shapas, T. J., and W. L. Hilsenhoff. 1976. Feeding habits of Wisconsin's predominant lotic Plecoptera, Ephemeroptera, and Tricoptera. Great Lakes Entomol. 9: 175–188.

Smyly, W. J. P., and V. G. Collins. 1975. The influence of microbial food sources and aeration on the growth of *Ceriodaphnia quadrangula* (O. F. Müller) (Crustacea: Cladocera) under experimental conditions. Freshwater Biol. 5: 251–256.

Sterba, G. 1953. Die Physiologie und Histogenese der Schilddrüse und des Thymus beim Bachneunauge (*Lampetra planeri* Bloch — *Petromyzon planeri* Bloch) als Grundlagen phylogenetischer Studien über die Evolution de innersekretor-ischen Kiemandarm Derivate. Wiss. Z. Friedrich-Schiller-Univ. Jena Math.-Naturwiss. Reihe 2: 239–298.

1961. Zur Phylogenese des Kiemendarmes der Chordaten. Int. Rev. Gesamten Hydrobiol. Hydrog. 46: 105–113.

1962. Die Neunaugen (Petromyzonidae), p. 263–352. *In* R. Demoll and H. Maier (ed.) Handbuch der Binnenfischerei Mitteleuropas. E. Sschwizerbart, Stuttgart.

Wigley, R. L. 1959. Life history of the sea lamprey of Cayuga Lake, New York. Fish. Bull. U.S. Fish. Wildl. Serv. 59: 559–617.

Young, J. Z. 1950. The life of vertebrates. The MacMillan Company, New York.

Blood Composition and Osmoregulation in Ammocoete Larvae[1]

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MORRIS, R. 1980. Blood composition and osmoregulation in ammocoete larvae. Can. J. Fish. Aquat. Sci. 37: 1665–1679.

Ammocoetes of all species are typical stenohaline freshwater animals which are able to regulate their blood and tissue ions very efficiently although they live in a very dilute environment. They excrete osmotic water by a well-developed kidney, and water turnover is high. Nephron units are sequentially arranged and have similar differentiated segments to those of other freshwater vertebrates. Total ion loss is low so the kidney must conserve ions efficiently. Ion loss is compensated by an ion-uptake mechanism, probably located in the interplatelet area of the gills. Here, the cells contain a sodium carrier whose transport rate is regulated by internal and external sodium levels; also they have mechanisms for potassium and chloride uptake. Both the gills and kidney have ion transport type cells, but the skin does not. The gills are probably the main access route for water, ions, and lampricides. The freshwater mechanism of osmoregulation persists beyond metamorphosis and thereafter many lampreys become euryhaline, but ammocoetes are unable to osmoregulate in hypertonic solutions and show passive responses. The adults of anadromous species like *Lampetra fluviatilis* and *Petromyzon marinus* develop a marine osmoregulatory mechanism which is similar to that of marine teleosts, whilst freshwater species like the landlocked *P. marinus* of the Great Lakes and the dwarf brook lamprey, *Lampetra planeri*, show reduced capacities for osmoregulation in seawater.

Key words: ammocoetes, lampreys, osmoregulation, blood composition, gills, ion fluxes, kidney, urine, water fluxes, ion compartments

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Les ammocètes de toutes espèces sont des animaux dulçaquicoles sténohalins typiques, capables de régler très efficacement leurs ions sanguins et tissulaires, bien qu'elles habitent dans un milieu fort dilué. Grâce à un rein bien développé, elles excrètent de l'eau osmotique, et le renouvellement d'eau est rapide. Les unités du néphron sont disposées à la suite et possèdent des segments différenciés semblables à ceux des autres vertébrés dulçaquicoles. La perte ionique totale est faible, de sorte que le rein doive conserver efficacement les ions. La perte d'ions est compensée par un mécanisme de captation d'ions, probablement situé entre les plaques branchiales. À cet endroit, les cellules contiennent un porteur de sodium dont la vitesse de transport est contrôlée par les niveaux interne et externe de sodium; elles possèdent également des mécanismes de captation du potassium et du chlorure. Les branchies et le rein ont tous deux des cellules assurant le transport des ions, mais la peau en est dépourvue. Les branchies sont probablement les principales voies d'entrée de l'eau, des ions et des lampricides. Le mécanisme d'osmorégulation d'eau douce persiste au-delà de la métamorphose, après laquelle plusieurs lamproies deviennent euryhalines, mais les ammocètes sont incapables d'osmorégulation dans des solutions hypertoniques et elles ont des réponses passives. Les adultes d'espèces anadromes telles que *Lampetra fluviatilis* et *Petromyzon marinus* acquièrent un mécanisme osmorégulateur d'eau salée semblable à celui des téléostéens marins, alors que les espèces dulçaquicoles telles que *P. marinus* confiné dans les Grands Lacs et la lamproie de ruisseau européenne naine, *Lampetra planeri*, ont une capacité d'osmorégulation limitée en eau salée.

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INFORMATION on the ionic constituents and osmoregulatory mechanisms used in freshwater by various species of lamprey is by no means complete, yet is sufficient to show that there is a very efficient homeostatic mechanism for controlling salt and water balance in ammocoete larvae, in landlocked metamorphosed stages, and in anadromous species returning to spawn in freshwater (Morris 1972; Robertson 1974). This article is mainly concerned with conditions in ammocoete larvae, but occasionally comparisons between larvae and lampreys will be made where appropriate. As larvae and, in later stages, lampreys face the general problems of life in freshwater where they maintain their ionic composition at a much higher level than that of their surroundings. This brings about osmotic intake of water and loss of ions, factors which are balanced by mechanisms located in the kidney and gills.

BLOOD COMPOSITION AND IONIC CONSTITUENTS

The most complete series of analyses from ammocoetes have been obtained from European brook lamprey, *Lampetra planeri*, the dwarf freshwater lamprey which ceases to feed after metamorphosis (Hardisty 1956; Bull and Morris 1967), from landlocked sea lamprey, *Petromyzon marinus*, from the Great lakes (Urist 1963: Urist and van der Putte 1967; Mathers and Beamish 1974), and from anadromous sea lamprey, *Petromyzon marinus* (Beamish et al. 1978). These analyses are collected in Table 1 together with corresponding data for adults in freshwater.

These studies show that both larval and adult lampreys maintain a lower blood osmotic concentration than many teleosts (Black 1957; Potts and Parry 1964) but the general pattern of osmotically active cations and anions is very similar in that sodium contributes 81–90% and chloride is responsible for 67–71%. There is no evidence for seasonal variation of osmotic concentration or ionic constituents of ammocoetes (Bull and Morris 1967; Mathers and Beamish 1974). There are insufficient data on *L. planeri*, but in landlocked and anadromous *P. marinus* there is a significant increase in osmotic concentration with size at metamorphosis, though the value decreases again towards spawning (Mathers and Beamish 1974; Beamish et al. 1978). The analyses of Urist (1963) and Urist and van der Putte (1967) for similar stages show that this increase is largely due to changes in sodium, potassium, and chloride concentration whilst the remaining ions change very little. Urist (1963) has shown that the adult lamprey is a typical freshwater vertebrate with regard to its serum calcium and phosphate levels, and later analyses (Urist and van der Putte 1967) indicate that the ammocoete is the same. In this respect, lampreys resemble freshwater teleosts and have the necessary concentration of ions to produce ossification, if they were biologically capable.

Some lamprey serum proteins appear to be unique and thus it may be inappropriate to apply the terminology developed during studies on other vertebrates.

Serum proteins rise after metamorphosis from 27 as ammocoetes to 39.0 $\mathrm{mg \cdot mL^{-1}}$ in migrating and spawning adults (Table 1). Total protein in adults amounts to about 40% of the levels recorded for teleosts and higher vertebrates, and may be partitioned into 27 $\mathrm{mg \cdot mL^{-1}}$ "albumin" and 12 $\mathrm{mg \cdot mL^{-1}}$ "globulin" (Urist and van der Putte 1967). In the same landlocked species Webster and Pollara (1969) record a large decrease in protein concentration (71.4%) as the animal matures, indicating a peak in serum protein concentration during the parasitic phase. Electrophoretic studies by Thomas and McCrimmon (1964) show that it is the "albumin" band (the fastest moving electrophoretic component) which is reduced when the parasitic adult becomes a prespawning migrant. This "albumin" has been identified as a glycoprotein by Nagano et al. (1976) and represents 54% of the total serum protein in *Entosphenus japonica*. The glycoprotein has a total molecular weight between 300 000 and 360 000 with a sedimentation coefficient of 12.2 Svedborg Units (*S*). It consists of two subunits and presumably acts as a metabolic reserve during the natural starvation which takes place during the spawning migration. Other electrophoretic bands may correspond to α-globulin, β-globulin, and γ-globulin (Thomas and McCrimmon 1964). The literature on lamprey immunoglobulins has been reviewed by Marchalonis (1977), who points out that lamprey serum antibodies may be unique in size and structure. Pollara et al. (1970) have purified an immunoglobulin from the α-globulin fraction of lampreys which has a molecular weight of 300 000 (9*S*). This molecule, which is capable of agglutinating human erythrocytes, could be a heavy chain polymer or may be unique (Litman et al. 1970). Lamprey serum also contains a very large (48*S*) natural agglutinin to horse erythrocytes which is more like an invertebrate agglutinin. It consists of subunits held together by disulfide bonds (Marchalonis and Edelman 1968). Lamprey bacteriophage antibody (Marchalonis and Edelman 1968) has more features in common with immunoglobulins of vertebrates since it consists of both light and heavy chains, but these are not covalently linked by disulfide bonds and are easily dissociated.

Blood pH varies between 7.2 and 7.6 at 15°C and the ionic strength of the serum is similar to that of teleosts. Under these conditions, chemical reactivity is relatively high and only 1.87 mmol $\mathrm{Ca^{++} \cdot L^{-1}}$ are ultrafilterable out of a total serum calcium level of 2.6 $\mathrm{mmol \cdot L^{-1}}$, as are 1.17 mmol $\mathrm{PO_4{}^{--} \cdot L^{-1}}$ from 1.31 $\mathrm{mmol \cdot L^{-1}}$ of total inorganic phosphate. Increased temperature and pH combined with lowered ionic strength tend to increase protein binding of calcium and phosphate ions (Urist 1963).

In parallel with the increased concentration of serum proteins during metamorphosis, there is also a rise in

TABLE 1. Ionic constituents of ammocoete larvae and lampreys. Values in roman type: mmol·kg⁻¹ water. Values in italics: mmol·L⁻¹. Values in parentheses: recalculated from source using tables in Diem and Lentner 1970.

	Osmotic concn. Δ°C or mOsmol·L⁻¹	Ionic composition											Proteins mg·mL⁻¹	Fats g·100 g⁻¹ tissue water	H_2O % fat-free wet wt	Author
		Na^+	K^+	NH_4^+	Ca^{++}	Mg^{++}	Cl^-	SO_4^{--}	HCO_3^-	P^{--}	Cat.	Anions				
L. planeri																
Ammocoete																
Plasma	(257)	113.8	9.1				93.8								85.6	Bull and Morris 1967
	(233)						*58*									Hardisty 1956
Whole animal		35.81	75.8				26.67							6.58	82.52	Bull and Morris 1967
							24.0							(5.74)	84.8	Hardisty 1956
Muscle		21.8	103				12.3							9.9	82.3	Bull and Morris 1967
							30									Hardisty 1956
Adult																
Serum	(239)						*101*									Hardisty 1956
Whole animal							55							(1.29)	86.8	
Muscle							*52*									
Landlocked *P. marinus*																
Ammocoete																
Serum		*103.0*	*3.40*		*2.40*	*1.60*	*91.0*	*0.10*	*6.00*	*1.30*	110.4	*98.4*	27.0			Urist and van der Putte 1967
	(258)															
Adult	(301)															Mathers and Beamish 1974
Serum (metamorphosed)		*134.0*	*4.00*		*2.40*	*1.80*	*122.1*	*0.10*	*5.00*	*1.30*	*142.2*	*128.5*	32.0			
(Parasitic)		*137.0*	*3.30*		*2.20*	*2.00*	*122.1*	*0.10*	*5.00*	*1.40*	*144.5*	*128.6*	35.0			Urist and van der Putte 1967
(Migrating and spawning)		*139.0*	*6.20*		*2.37*	*1.90*	*113.0*	*0.87*	*5.18*	*1.40*	*149.47*	*120.45*	39.0			Urist 1963
(Spawning)		*136.0*	*5.10*		*2.74*	*1.75*	*112.0*	*0.74*	*5.21*	*1.31*	*145.59*	*119.26*				
	257															Mathers and Beamish 1974
Anadromous *P. marinus*																
Ammocoete																
Serum	225	101					76									Beamish et al. 1978
Adult																
Plasma (fresh-run)	0.495 (267)	*111.9*	*2.3*		*1.8*	*1.5*	*99.6*			*2.5*	*117.5*					Pickering and Morris 1970
	0.540 (292)						*119.0*			*1.8*						Fontaine 1930 Fontaine 1932
(mature)	285															Beamish et al. 1978

TABLE 2. The body-fluid compartments of ammocoete larvae (July) compared with those of other aquatic vertebrates.

Compartment	*L. planeri* ammocoete (3 g)[a]	*P. marinus* adult (190 g)[b]	Elasmo-branch[b]	Freshwater teleost[c]
Haematocrit (blood cells as a % of whole blood)	38.61 ± 1.43 (6)	33.0	18.3	32
Blood volume (% body wt.)	7.97 ± 0.66 (6)	8.5	6.6	2.8
Plasma volume (% body wt.)	4.84 ± 0.48 (6)	5.5	5.4	1.8
Extracellular volume (% body wt.)				
(a) Inulin sp.	24.41 ± 1.26 (5)			
(b) Sucrose sp.	22.3 (2)	23.9	21.2	14.0
Interstitial sp. (% body wt.)	19.57	18.4	15.8	12.2
Muscle blood volume (% wet wt.)	6.33			

[a] Bull and Morris 1967.
[b] Thorson 1959.
[c] Thorson 1961.

haemoglobin concentration and haematocrit values for landlocked *P. marinus* ammocoetes from 5.6 g · 100 mL^{-1} and 22.1%, respectively, to peak values of 10.9 g · 100 mL^{-1} and 44.7% at the begining of the spawning run (Potter and Beamish 1978). Values for the haemacrit of other ammocoete species are higher (*Ichthyomyzon hubbsi*, 24%, Potter et al. 1970; landlocked *P. marinus*, 28.7%, Beamish and Potter 1972; *L. planeri*, 38.6%, Bull and Morris 1967) and indicate a great deal of variation in this respect.

Blood glucose levels in *L. planeri* ammocoetes amount to 49.65 ± 1.76 mg · 100 mL^{-1} of blood when measured under carefully controlled conditions (Morris and Islam 1969), and this is equivalent to 2.8 mOsmol · L^{-1}. Thus, even in diuretic conditions when the blood glucose of larvae approach the renal threshold (estimated at 70–80 mg · 100 mL^{-1}) the osmolarity would only be expected to increase by 4.4 mOsmol, and this is unlikely to be a significant increase from the osmotic point of view.

FLUID AND IONIC COMPARTMENTS OF WHOLE AMMOCOETES AND TISSUES

Attempts have been made to assess the fluid compartments of *L. planeri* ammocoetes (Bull and Morris 1967), adult *P. marinus*, and members of other fish groups (Table 2). The values for blood and plasma volume and extracellular and interstitial space are very similar in both larvae and adults in spite of large differences in size. The large blood volumes of lampreys and elasmobranchs are said to be characteristic of primitive fish and are brought about by the presence of large blood sinuses (Thorson 1959).

Table 3 contains a summary of some of the ionic compartments in ammocoete larvae of *L. planeri* and their muscles, which represent 75% of the body weight of the animal (Bull and Morris 1967). The ionic compartments have been measured by dividing the total amount of ion within the animal by its concentration in the serum. Thus, chloride space amounts to 285 mL · kg^{-1} of water which is almost the same as the extracellular space of the animal as measured by labeled inulin (284 mL · kg^{-1} water), and this indicates that the cells contain very little chloride. Sodium is also kept at a low level within cells and according to isotopic experiments employing ^{24}Na about 50% of the cellular sodium is exchanged in 2–3 h.

The sodium/potassium ratio for the extracellular fluid is 12.5 : 1, whilst the tissues show typical vertebrate characteristics with an inverse relationship in which the potassium/sodium ratio is 21.2 : 1. A potassium/sodium ratio of 14.8 : 1 for ammocoete muscle and the virtual lack of chloride from cells indicates that the ammocoete has extremely well-developed powers of ionic regulation at the cellular level, far better than the brown trout (12.8 : 1, Gordon 1959) or the rat (9.5 : 1, Conway 1945).

WATER BALANCE

Osmotic water is removed as a dilute urine in freshwater cyclostomes and fishes (Morris 1956; Potts and Parry 1964). Because of the difficulty of collecting urine from small animals like ammocoetes (Bull and Morris 1967), an indirect method has been devised that involved measuring the loss of weight which takes place when ammocoetes were transferred abruptly to isotonic solutions. Under these circumstances, osmotic uptake of water ceases, but the kidney continues to produce urine until it gradually adapts to new conditions. The initial weight loss from 2- to 3-g animals in isotonic solutions indicated urine outputs of 198 ± 20.5 mL · kg^{-1} · d^{-1}, much lower values than those obtained by Hardisty (1956) for adult *L. planeri* (1300 mL · kg^{-1} · d^{-1}) and *L. fluviatilis* (300 mL · kg^{-1} · d^{1}). Hardisty's method involved ligaturing the urinary papillae and then following the ensuing increase in

TABLE 3. Ionic compartments in ammocoete larvae (July) of *L. planeri* (calculated values are shown in italics).

Whole larva	Ionic content (mol·kg⁻¹ water)	Concn. (mol·kg⁻¹ water)	'Space' (mL·kg⁻¹ water)
Total Na	35.81	113.78	*314.7*
Exchangeable Na	*34.40*	113.78	303
Bound Na	*1.41*	—	—
Total Cl	26.67	93.76	*285*
Extracellular space			284
Extracellular Na	*32.39*	113.78	284
Intracellular Na	*3.42*	*4.78*	716
Bound Na	1.41	*2.02*	716
Total K	75.80	—	—
Extracellular K	*3.20*	9.14	284
Intracellular K	72.60	*101.2*	716
Extracellular Cl	*26.58*	93.76	284
Intracellular Cl	0.09	0.13	716
Muscle			
Total Cl	12.26	93.76	*130.8*
Total Na	21.76	113.78	*191.0*
Extracellular Na	*14.88*	113.78	130.8
Intracellular Na	6.88	*7.92*	869.2
Total K	102.97	—	—
Extracellular K	1.12	9.14	130.8
Intracellular K	101.85	*117.2*	869.2

weight. This gives very high values compared with those obtained using other methods for various species (*L. fluviatilis*: 155.8 ± 9.9 mL·kg⁻¹·d⁻¹, Morris 1956; *P. marinus*: 159 mL·kg⁻¹·d⁻¹, Sawyer 1955).

Comparisons of urine output are complicated by handling diuresis (Morris 1956), the use of anaesthetics (Hardisty 1956), and the temperature at which the measurements are made, since urine output increases with temperature (Wikgren 1953). The problem of comparing water permeabilities between different stages and species in freshwater is also complicated by the fact that we have no assessment of the relative permeabilities of the gills and skin and hence the assumptions which are made can lead to very different conclusions. Thus, comparisons of the mean osmotic permeability of larval *L. planeri* ammocoetes (0.47 $\mu m^3 \cdot \mu m^{-2} \cdot s^{-1}$) and adult river lampreys (0.42 $\mu m^3 \cdot \mu m^{-2} \cdot s^{-1}$) at 12°C, based on total surface area and the isotonic weight loss method described earlier, might lead to the conclusion that different stages and species have similar permeabilities in freshwater and thus that differences in urinary volume are due to different surface area/volume relationships. If, however, we make the more likely assumption that only the gills are permeable to water, the figures become 0.82 $\mu m^3 \cdot \mu m^{-2} \cdot s^{-1}$ for the ammocoete and 0.55 $\mu m^3 \cdot \mu m^{-2} \cdot s^{-1}$ for adult *L. fluviatilis* leading us to the conclusion that ammocoete gills are more permeable to water than the adult (R. Morris and M. Andrews unpublished data).

Attempts have also been made to measure the diffusional water permeability of ammocoetes using tritiated water (Andrews 1974) which gave rate constants [K(h⁻¹)] of 1.24 for influx and 1.46 for outflux. These figures, which measure the fraction of the exchangeable water compartment changed per hour, indicate a very rapid rate of water exchange for ammocoetes. Calculations based on measurements of influx show that the total body water is exchanged about once every 48 min. Calculations based on outflux measurements give a slightly higher rate of exchange (41 min) and may either indicate a difference in diffusional permeability of the membranes depending on the direction of water passage (Dainty and House 1966) or a difference in the relative efficiency with which water is circulated on the inside (vascular circulation) or the outside of the gills or skin. The adult brook lamprey (*K* for outflux = 1.31) exchanges water at a slightly lower rate (48 min) than its ammocoete.

ION BALANCE

Wikgren (1953) first drew attention to the ion balance problem of the adult lamprey living in freshwater; ammocoete larvae face similar problems. As in most freshwater vertebrates, ions may be lost as a result of a considerable concentration gradient across the external surfaces (Table 1) which are imperfect barriers to diffusion. In addition to this, ionic loss may also take place from the kidney where high rates of urine output result in some ion loss over this route in spite of a very efficient ion-conserving mechanism. The adult kidney manages to conserve 91–96% of the filtered sodium, 42–82% of filtered potassium, and 94% of the chloride from the glomerular filtrate (Morris 1972) resulting in maximum loss rates of 5.1, 0.98, and 1.8 mmol·kg^{-1}·d^{-1} for Na$^+$, K$^+$, and Cl$^-$. Unfortunately, there are no comparable figures for renal function in ammocoete larvae because of the difficulties involved in collecting and analyzing small amounts of urine.

However, other aspects of ion balance have been studied in ammocoetes. Ion loss from the external surfaces and the kidney are compensated by an efficient ion uptake mechanism (Hardisty 1956; Morris and Bull 1968, 1970; Pickering 1973). The mechanism has been shown to be located in the gills by partial immersion experiments (Kaye 1963) and by autoradiographic studies (Patinawin 1967).

Estimates of sodium loss have been made by following sodium losses in distilled water (Morris and Bull 1968). The experiments have taken two forms. In the first type, sodium equilibria have been followed at normal temperatures (10°C). Ammocoetes become progressively more efficient at preserving sodium balance at each successive reimmersion in deionized water. The system becomes more effective when the animal has lost 20–40% of its total body sodium and presumably indicates an increase in the efficiency of sodium uptake. The lowest concentration of sodium at which sodium balance can be obtained is known as the minimum equilibrium concentration for sodium and represents the maximum efficiency with which ion balance can be achieved. The value for ammocoetes lies between 5 and 30 μmol Na$^+$·L^{-1} and is lower than that demonstrated for other freshwater animals (crayfish, 9–20 μmol Na$^+$·L^{-1}, Shaw 1959; roach (*Leuciscus*), 20 μmol Cl$^-$·L^{-1}, Krogh 1937).

In the second type of experiment (Morris and Bull 1968), a combination of sodium loss in deionized water and simultaneous lowering of the environmental temperature have been used to assess ion loss, the low temperature serving as a metabolic inhibitor of the active transport of sodium. Under these circumstances, values for sodium loss are 0.115 μmol Na$^+$·g^{-1}·h^{-1}, somewhat higher than the results obtained from normal animals in later experiments (Morris and Bull 1970). The authors attributed this to the low levels of calcium which accompanied experiments of this type, as well as the fact that low temperatures reduce sodium loss to three-quarters of the normal value. In addition, influx was unable to take place, even at 10°C, until the losses were sufficient to raise the external sodium to the required minimum equilibrium concentration. Calcium levels in the environment had a pronounced effect on both sodium loss and uptake rates.

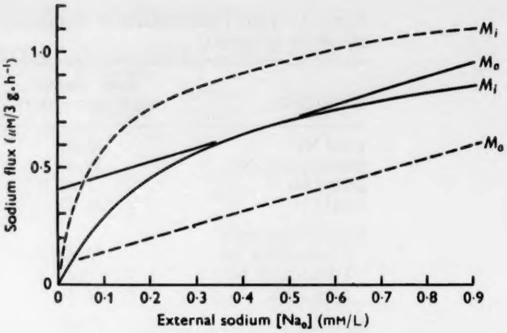


FIG. 1. The relationship between sodium influx (M_i), sodium outflex (M_o), and external sodium concentration ([Na$_o$]) in normal (continuous lines) and sodium-depleted (broken lines) *L. planeri* ammocoete larvae (from Morris and Bull 1968).

Thus the main factors involved in promoting a negative sodium balance in experiments of this type seem to be an almost complete inhibition of uptake by low temperature, a slight decrease in loss due to low temperature which is overshadowed by diuretic losses and the increase of sodium loss due to very low levels of calcium. As a result sodium and chloride move from the extracellular space and potassium is lowered in muscle cells (Morris and Bull 1968). The value of these experiments is that they provide a method of deionizing animals rapidly without apparent physiological damage since the animal is able to regain sodium rapidly when returned to dilute solutions containing the requisite ions, e.g. Ringers solution diluted 100 times with distilled water (R/100).

Using methods of this type it has been possible to compare the differences associated with kinetics of sodium transport in deionized and "normal" ammocoete larvae of the brook lamprey (Morris and Bull 1970). These experiments (Fig. 1) were performed by following the responses of individual animals, i.e. measuring sodium influx (Mi) by ^{24}Na and calculating outflux (Mo) from a knowledge of netflux (Mnet) and Mi, as the animal was moved to progressively increasing sodium concentrations made up in (R-Na)/100.

The influx curves for both groups of animals show saturation type kinetics, which would indicate a sodium carrier mechanism of limited capacity, transporting molecules inward. Sodium depletion results in an increase of sodium transport which not only increases Mi but may also reduce Mo by back transporting outfluxing sodium ions before they leave the vicinity of the transport mechanism at the gills. It is these factors which are responsible for the rapid return to normal sodium balance, where Mi and Mo balance for a particular environmental sodium concentration. Sodium influx and the level of plasma sodium (P) are negatively correlated ($P = 0.05\ Mi + 5.22$), but there is some individual variation (Morris and Bull 1970).

Similar mechanisms have been described for other freshwater animals (crayfish, Shaw 1959; frog skin, Kirschner 1955). Shaw (1959) was the first to point out how a similar mechanism used by crayfish could be virtually self-regulatory in response to changes in ion levels in the environment or to changes of permeability on the part of the animal. Thus, an animal in sodium balance at 0.4 mmol $Na^+ \cdot L^{-1}$ moves to a more dilute environment, e.g. 0.2 mmol $Na^+ \cdot L^{-1}$ and loses sodium because of the disparity between influx and outflux. The lowered level of internal sodium now increases sodium uptake and reduces sodium loss resulting in sodium balance at the new level. Conversely, a move to a higher sodium environment might be expected to reduce influx and increase outflux to balance the animal at the higher level. In a system of this type, it is the affinity of the carrier for sodium rather than low sodium permeability which enables animals to live in dilute sodium solutions.

Changes in sodium influx could be brought about in one of two ways. The first appears to be a short-term response involving a change of affinity of the carrier. The half-saturation constant for influx (Ks) is low for normal animals ($Ks = 0.13$ mmol $Na^+ \cdot L^{-1}$) but higher for sodium-depleted animals ($Ks = 0.26$ mmol $Na^+ \cdot L^{-1}$) implying a change of carrier affinity with sodium level. The second way of altering influx would be to increase the amount of carrier and, since this is likely to involve biosynthesis, the process is more likely to be a long-term one, perhaps involving hormonal control.

It is interesting that Pickering (1973), by careful handling and adaptation of his animals, managed to obtain sodium balance in *L. fluviatilis* ammocoetes at much lower flux rates (0.08 $\mu mol \cdot g^{-1} \cdot h^{-1}$) than those achieved by our "normal" animals when in sodium balance (0.2 $\mu mol \cdot g^{-1} \cdot h^{-1}$). Whilst there is the possibility that our "normal" animals were stressed in spite of the careful handling they received, it may be that the lower temperature used by Pickering (8–9°C), lower sodium values for the environment (0.2 mmol $Na^+ \cdot L^{-1}$), and the higher environmental calcium levels (0.18 mmol $Ca^{++} \cdot L^{-1}$) he employed would all tend to reduce sodium outflux. Whatever the reason for these differences, it illustrates that ammocoetes are able to balance sodium successfully with very different sodium permeabilities and that sodium turnover can vary from as little as 6.5% of the total body sodium per day (Pickering 1973) up to 18.4% (Morris and Bull 1970).

THE MAIN ORGANS AND TISSUES INVOLVED IN OSMOREGULATION

The kidney — Whilst the ammocoete faces continuous problems of water excretion and ion conservation in freshwater, the kidney is a continuously changing structure. The rudimentary pronephros copes with the problems in young larvae and the larval mesonephros takes over at the burrowing stage (9–12 mm long). This structure gradually increases in length and complexity as the larvae grows, adding new tubules posteriorly whilst anterior ones regress. Eventually at metamorphosis the larval mesonephros is replaced by a larger, more tightly organized adult structure, which in some cases functions as an organ of marine osmoregulation. During the spawning run in freshwater, the kidney again changes its function to that of volume regulation and ion conservation. It finally regresses at sexual maturity. The earlier studies, which concentrated on the structures involved, and the development of this complex series of events are summarized in articles by Pietschmann (1933), Gérard (1954), Morris (1972), and Ooi and Youson (1976). The account which follows concentrates on more recent studies which describe the functional mesonephros (opisthonephros) of the ammocoete.

The functional pronephros develops within the pericardial coelom and its large glomeruli on each side of the dorsal aorta are presumed to produce coelomic fluid by ultrafiltration. The fluid is thought to be taken up by the open nephrostomes of the pronephric tubules (6–8), passed through the winding tubules where the fluid may be modified and eventually passed into the pronephric duct to be voided at the cloacal region. As the larval mesonephros develops, so the pronephric tubules and the pronephric duct regress, but they may still function as an organ of storage excretion in older larvae (Torrey 1938).

The larval mesonephros or opisthonephros (Kerr 1919; Youson and McMillan 1970a) develops anteriorly from the paired cords of nephrogenic tissue which extend the length of the animal on each side of the dorsal midline within the perivisceral coelom (Wheeler 1899). At this stage, each nephron unit consists of a blind convoluted tubule, the end of which becomes modified to form the flattened epithelium of Bowman's capsule, and this associates with the developing capillaries of the glomera derived from branches of the renal artery. This process continues caudally until large numbers of tubules are formed and open into the pronephric duct.

The larval mesonephros appears to grow throughout the length of the life of the larva and, as the strap-like kidneys lengthen, the number of glomera and their draining nephron units increase at the caudal end of the kidney (Wheeler 1899; Youson and McMillan 1970a). The growth appears to be periodic according to Ooi and Youson (1976), who found that kidney growth took place rapidly during the first 3 yr of larval life and thereafter remained relatively constant. Thymidine labeled with ^3H showed that the nephrogenic tissue continued to produce new nephron units until the 3rd yr of larval life and that from then on,

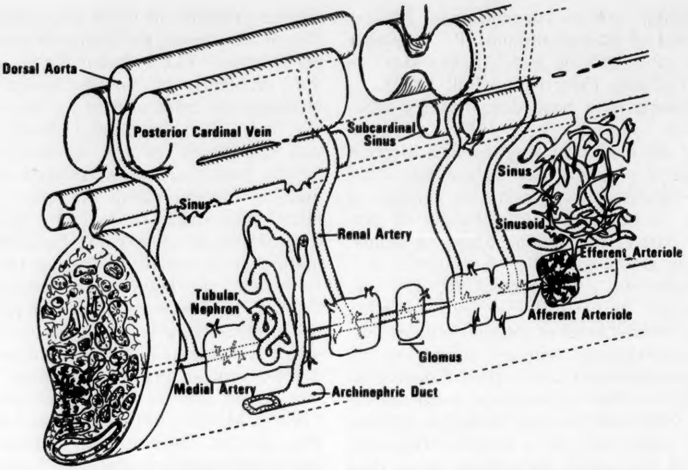
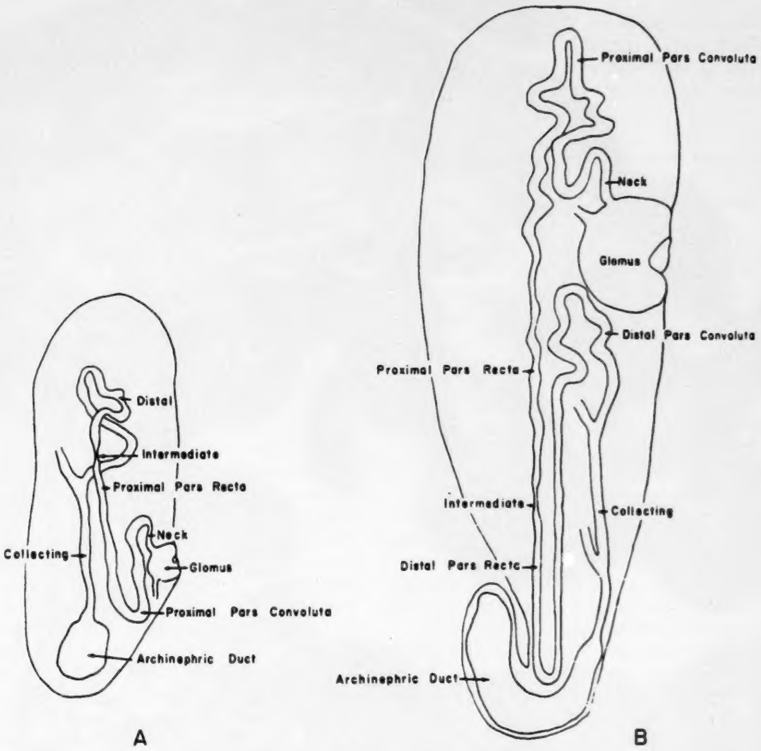


FIG. 2. Portion of the opisthonephros of a 125-mm ammocoete showing its vascularization. Blood is traced from the dorsal aorta through the renal and medial arteries to enter the glomus through afferent arterioles. It leaves through efferent arterioles which enter into capillaries (not shown) and then sinusoids. Blood from these intertubular sinusoids drains into the subcardinal sinus dorsally through a short sinus. The subcardinal sinus periodically drains into the posterior cardinal vein (from Youson and McMillan 1971d).

growth consisted of elongation of existing nephron units by cell proliferation. Posterior growth of the ammocoete kidney is also accompanied by anterior degeneration (Youson 1970). Each glomus consists of a compound glomerulus (Fig. 2) in which a branch of the renal artery divides into a number of afferent arterioles (3–11) each giving rise to an anastomosing network of capillaries, each drained by its own efferent arteriole (Youson and McMillan 1970a). Each capillary loop is invested by its own Bowman's capsule drained by a separate nephron unit. As development proceeds and the glomera increase in numbers posteriorly, so they tend to form long continuous blocks in older ammocoetes. These may be supplied by as many as three renal arteries joined to a medial artery, running the length of the glomerula block and from which the capillary loops of separate glomeruli may be derived (Fig. 2). Frequently the double Bowman's capsule invests adjacent capillary loops and hence lies between them. Ultrastructural studies (Youson and McMillan 1970a) show that the endothelial cells of the capillary loops rest on a continuous basement membrane which is surmounted by a layer of podocyte cells to form a visceral layer. These irregular cells have a large number of branching cytoplasmic processes which rest on the basement membrane, and the visceral edges of the capsule continue as a second parietal or squamous layer which eventually drains into the neck segment of the nephron.

The remaining components of the nephron are illustrated in Fig. 3 which draws attention to the fact that the ammocoete nephron unit has five differentiated segments like the adult unit which replaces it at metamorphosis, but the arrangements of the units are quite different within the two kidneys (Youson and McMillan 1970b). Each nephron consists of a short ciliated neck segment, a brush-bordered proximal segment in which the convoluted portion has taller cells, higher brush borders, and a larger lumen than the straighter section which follows it. Ultrastructural details suggest that this segment has an absorptive function (Youson and McMillan 1970b) and may be similar to that of other vertebrates in conserving glucose, amino acids, and macromolecules.

A short, nonciliated intermediate segment leads to a longer distal segment in which the smaller flattened cells contain numerous mitochondria and well-developed, smooth, endoplasmic reticulum. Some cells (dark cells) are unusual in possessing large amounts of glycogen whilst others (light cells) are similar to those of the same segment in adults. Like the proximal segment there are no infoldings of the basal plasma membrane such as are present in distal cells from many vertebrates (Youson and McMillan 1971a). The collecting segment drains two or more nephron units and may join with others into a straight, common, collecting segment which eventually leads directly into the archinephric duct. Like the distal tubules, the collecting duct cells contain abundant mitochondria and smooth endoplasmic reticulum which suggests that like the distal cells, they are likely to have an ion-absorbing function. Ion absorption would be expected to be ac-


Distal
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Distal Pars Recta
Archinephric Duct
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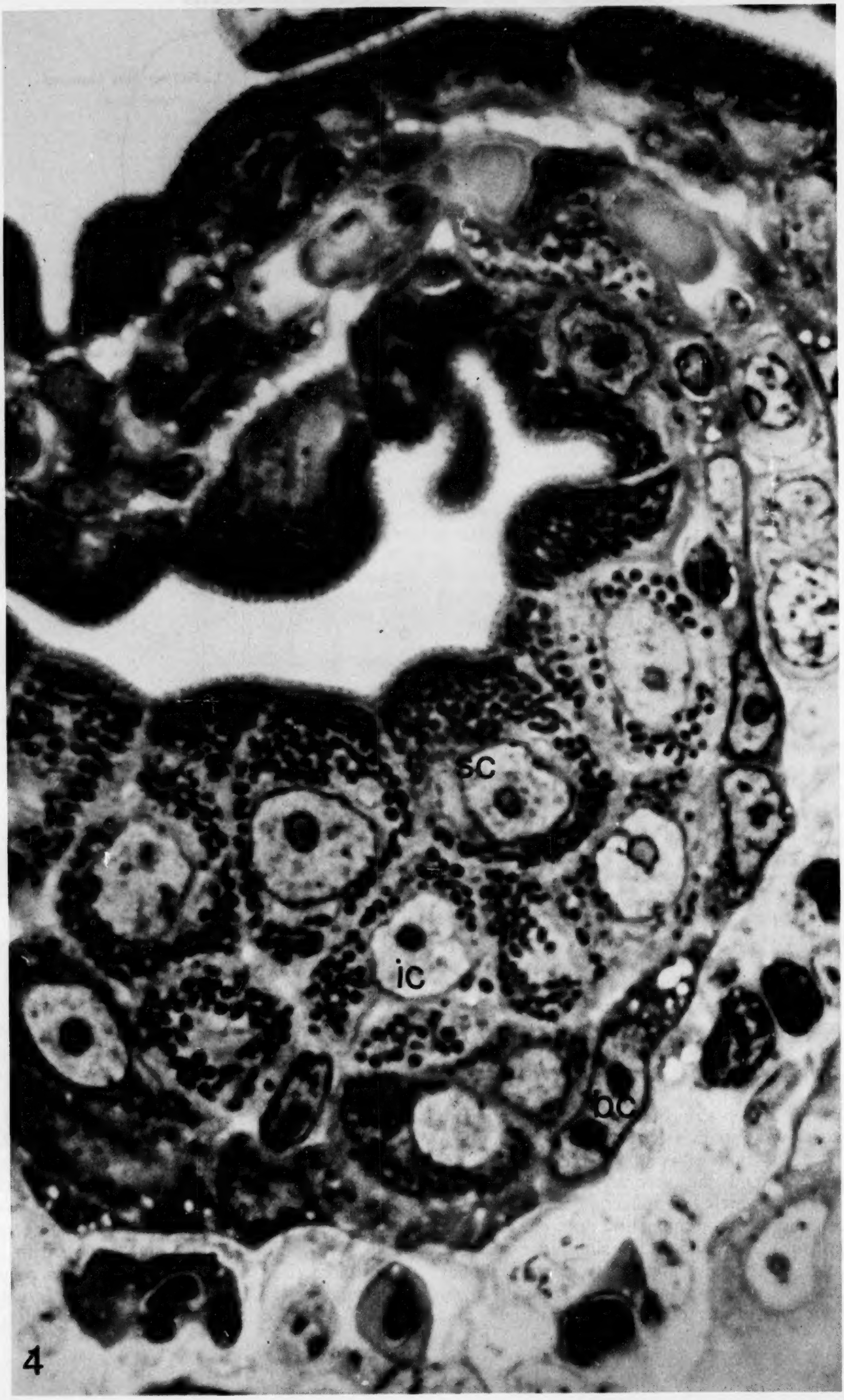
FIG. 3. A comparison of the tubular nephron of the ammocoetes (A) and adult (B) of the Great Lakes sea lamprey. The location of the various segments in these diagrams of cross sections of the kidney is related to the position of the glomus (from Youson and McMillan 1970b).

companied by osmotic absorption of water because of the osmotic gradient between the contents of the tubule and the blood surrounding the tubule.

It is interesting in this respect that Logan et al. (1980) have conducted micropuncture studies on the kidney of *L. fluviatilis* in freshwater and have shown that the majority of Na^+, K^+, and Cl^- reabsorption takes place in the distal tubule whose cells, whilst showing minor differences from the cells of ammocoetes (Youson and McMillan 1971b), have the main features of ion-absorptive cells (i.e. abundant mitochondria and smooth endoplasmic reticulum). Whether this function is likely to continue into the collecting ducts and the archinephric duct of the ammocoete, into which the collecting ducts drain, is an open question. The archinephric duct consists of a thin-walled tube surrounded by sinusoids, and the anterior part of the duct appears to contain similar cells to those of the collecting ducts. The cells from the posterior end of the duct are more variable but again contain organelles which suggest capacities for ion absorption (Youson and McMillan 1971c).

The functional kidneys of both ammocoete and adult lack a renal portal system (Fig. 2). In ammocoetes, blood arising from the efferent anterioles of the capillary loops is routed into sinusoids between nephron units and eventually drains into a subcardinal sinus before it is returned to the general circulation by way of the posterior cardinal vein (Youson and McMillan 1971d).

Hoar (1966) believes that the renal portal system in fish is a device for water conservation, in which glomerular filtration could be reduced whilst maintaining the venous supply to the tubules from the portal system so that tubular secretion could continue unhindered. This type of system could be of some significance during marine osmoregulation in teleosts, where glomerular filtration rate could be reduced by glomerular recruitment and yet tubular secretion continue in those tubules with low filtration rates. If this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is true, lack of a renal portal system should have no significance during freshwater osmoregulation in both larval and adult lampreys where tubular secretion may play little part in kidney function (Morris 1972). The situation during seawater osmoregulation may be quite different, however, where urine output is low and divalent ion excretion high (Pickering and Morris 1970). It remains to be shown how the marine lamprey kidney manages to obtain similar end results to those produced by the kidney of marine teleosts, in spite of anatomical differences.

The skin — The soft skin of both ammocoete and adult lampreys is similar in that each consists of a multilayered epidermis separated by a dense, collagenous, dermal layer from a pigmented layer which lies on top of connective tissue containing blood capillaries and fat cells. In larvae and adults, there are similar cellular constituents in the epidermis, i.e. three or four layers of mucous cells at various stages of development, separated by large intercellular spaces and terminated by mature cells with stored mucus and a pronounced brush border. Club-shaped cells, with twin nuclei within a central cytoplasmic cone, are surrounded by layers of tonofibrils, whilst granular cells, joined to the dermis by a thin cytoplasmic strand, contain large numbers of lipoprotein granules (see Morris 1972 for a more detailed review). So far, there is little certainty about the function of the latter two cell types. Ultrastructural studies (Downing and Novales 1971a, b, c) lend no support to the ideas of Pfeiffer and Fletcher (1964) that club-shaped cells are stages in the production of granular cells. The latter may, however, as Pfeiffer and Fletcher suggest, contain a secretion distasteful to predators. They could also be the source of the peptides discovered by Fischer and Albert (1971), who describe bradykinin-like activity from skin extracts. Downing and Novales could find no evidence for nervous connections to the club cells to support the idea that they may be sense organs. Anderson and Manion (1977) have shown that the ventral body wall increased in thickness when newly metamorphosed lampreys became parasitic. The club-shaped cells lengthen, whilst the granular cells stay in the upper half of the skin as the epidermis doubles in thickness. There is also a fourfold increase in the dermal collagenous layer and a fivefold increase in the fat layer which lies beneath this. These layers presumably act as a food store, since they decrease by 36 and 60% in the prespawning lamprey. At this time the club cells shorten and granular cells are distributed throughout the width of the epidermis (Anderson and Manion 1977).

The river lamprey (*L. fluviatilis*) shows an increase in water permeability as it enters freshwater on its spawning migration (Morris 1956) and it would be interesting to know whether there is any relationship between change of skin structure and water permeability at this time.

The gills — Accounts of gross morphology of the gills of ammocoete larvae are given by Sterba 1953, 1961; Morris 1972; Lewis and Potter 1975, and Youson and Freeman 1976.

The organization of the gill pouches in ammocoetes is different from the adult. They consist of a series of structures (holobranchs) which lie between each gill pore (Lewis 1980). Each holobranch consists of an anterior and posterior plate (hemibranch) held together by connective tissue septum which joins to the body wall and hence separates the gill into incomplete pouches. Each plate consists of 11 or 12 horizontal filaments, stacked one above the other, and attached to the branchial bar within the pharynx at one end, but lying relatively free at the other.

The filaments have 30 to 40 perpendicular platelets (lamellae) on each side and these are arranged transversely to face one another on adjacent filaments. Blood from the ventral aorta is fed to the afferent branchial arteries within the septa of the holobranchs and then distributed to afferent filamentar vessels on the inner edge of the gill filament. Flat filamentar blood vessels convey the blood to the platelets and corresponding efferent vessels drain the blood to the dorsal aorta. Studies on the cytology and ultrastructure of the gill epithelium of ammocoete larvae show that the platelets are covered by a single layer of flattened platelet cells, which is consistent with the hypothesis that they are involved in gaseous exchange (Fig. 4). The areas between platelets, however, contain layers of cells packed with mitochondria which are continuously replaced from a basal cell layer (Kaye 1963; Patinawin 1967; Morris and Pickering 1975; Youson and Freeman 1976).

Autographic studies, using a method to localize ions (modified from Pelc and Appleton 1965), have shown that $^{22}\mathrm{Na}^{+}$, $^{42}\mathrm{K}^{+}$, $^{45}\mathrm{Ca}^{++}$, and NH_4^{+} enter the gills rapidly when presented as chloride, whilst $^{131}\mathrm{I}^{-}$, $^{32}\mathrm{P}^{--}$, $^{36}\mathrm{Cl}^{-}$, and $^{35}\mathrm{SO}_4^{-}$ enter equally rapidly as sodium salts (Patinawin 1967; Morris 1972). Our interpretation of this is that there are mechanisms for transporting sodium, potassium, and chloride in ammocoete gills which will work independently. Sulfate will enter the gills as a sodium or potassium salt, but not when presented with ammonium or calcium ions. Thus there are unlikely to be mechanisms for transporting calcium, ammonium, and sulfate ions. Tritiated water and the ion combinations which penetrate the

FIG. 4. Interplatelet area of the gills from a *L. planeri* ammocoete. Note the numerous mitochondria-rich cells (bc, basal cell; ic, intermediate cells; sc, superficial cell). Glutaraldehyde–osmium, toluidine blue × 2500 (from Morris and Pickering 1975).

gills show little sign of entering the skin unless this has been damaged. The interplatelet areas show very little sodium or chloride in these experiments, though the platelet and interplatelet blood vessels are heavily loaded. We conclude, therefore, that the interplatelet cells, like muscle cells, contain little sodium or chloride, and so transport of ions must be very rapid.

There have been two independent investigations on the ultrastructure of ammocoete gills (Morris and Pickering 1975; Youson and Freeman 1976) and there seems to be agreement that the thin platelet cells are involved in respiratory exchange. These cells have microvilli on their free borders and are coated with an amorphous material which is probably mucus. The interplatelet (interlamellar) area contains at least three layers of cells (Fig. 4); basal, intermediate, and superficial cells, and there appears to be an increase of mitochondrial content in the larger superficial cells which border the interplatelet area. The occasional "light cells" mentioned by Youson and Freeman probably correspond to the degenerating superficial cells described by Morris and Pickering. In these cells, the Golgi apparatus buds off membrane-bound vesicles which swell as degeneration proceeds. The mitochondria also swell until they are almost unrecognizable. Both groups of authors agree that the mitochondrial-rich cells are probably responsible for the active uptake of ions; but Morris and Pickering, working on *L. fluviatilis* and *L. planeri* ammocoetes, could not identify the smooth endoplasmic reticulum which is so characteristic of many ion-transporting cells of gills. This organelle only appeared in replacement cells later in development during and after metamorphosis (Pickering and Morris 1976; Morris and Pickering 1976). Youson and Freeman claim that the cells of *P. marinus* ammocoetes have abundant, smooth, endoplasmic reticulum.

Thus the gills of ammocoetes are likely to perform the dual function of promoting gaseous exchange and absorbing ions. Czopek and Sawa (1971) estimated the relative vascularization of gills and skin of adult *L. fluviatilis* to be 92 and 8% and pointed out that deeper skin capillaries are less likely to be efficient during respiration. These findings are also consistent with the view that the gills are likely to be the main route for the exchange of water and ions during osmoregulation.

It is interesting in this connection that Christie and Battle (1963) found that the gills of both ammocoete larvae and trout were heavily vasodilated after treatment with the specific lampricide 3-trifluormethyl-4 nitrophenol (TFM) and that edema also occurred between the gill epithelium and the capillary endothelium. In ammocoetes, the vasodilation extends to the liver and posterior hindgut, whilst edema also affects skeletal muscle. In most ammocoetes and adult lampreys, large mucous cells are present in the cells of the gill chamber between the base of the gill filaments and at their tips (Sawyer 1959). Whether these produce the mucus which normally covers the epithelial surfaces, or whether this is produced by some of the platelet and interplatelet cells themselves, is equivocal. The large mucous cells discharge into the branchial cavity on treatment with TFM (Christie and Battle 1963) or *N*-4-nitrophenyl-4 chlorobenzene (Sawyer 1959), and it is mainly those on the filament tips which discharge. Christie and Battle conclude that TFM enters the body through the gills since it appears to have little effect on the mucous cells of ammocoete skin.

OSMOREGULATORY ABILITY IN HYPERTONIC SOLUTIONS

A number of attempts have been made to adapt various species of ammocoete larvae to seawater dilutions of different concentrations. In all cases, the ammocoetes have managed to cope in blood hypotonic solutions, hence there is clear evidence that they are physiologically freshwater animals. The ability to osmoregulate in blood hypertonic solutions does not develop until the early macropthalmia stage which follows metamorphosis, and it is at this time that far-reaching morphological and physiological changes take place, which enable the animal to resist the desiccating effects of seawater. At this stage, the animal is able to use a swallowing-extra-renal excretory mechanism, similar to that used by teleosts, to keep the blood hypotonic to the more concentrated environment. Details of these studies are reported elsewhere in this Symposium (Youson 1980; Beamish 1980).

We know most about the plight of the ammocoete in different seawater dilutions from investigations by Mathers and Beamish (1974) on landlocked *P. marinus* ammocoetes from the Great Lakes, and those studies conducted by Beamish et al. (1978) on anadromous *P. marinus*, which make it possible to compare the relative performance of the two species in different seawater dilutions. The comparison shows that the landlocked form continues to remain hypertonic to its environment, and at 10‰ (~31% seawater) the osmolarity had increased by more than 80 mOsmol·L^{-1} (see Beamish 1980). It therefore seems that these ammocoetes were tolerating the increased osmotic stresses brought about by their environment and the expectation would be that they would not survive. In contrast to this situation, anadromous *P. marinus* larvae appeared to keep their blood osmotic pressure low until they reached isotonicity at about 12‰ seawater (about 38% seawater). Deaths from prolonged exposure at 10‰ in 6–7 d and earlier deaths at higher salinities for the same species suggest that, although there may be a more positive response to higher salinities in anadromous species (e.g. a lower water permeability or an earlier cutoff for sodium absorption), there is no evidence for the existence of a coordinated marine mechanism such as that shown by adults.

Attempts to acclimatize larval and adult brook lampreys (*L. planeri*) to increasing concentrations of seawater (Hardisty 1956) gave no signs of a marine mechanism. Animals became isosmotic in concentrations of $140\ \text{mmol NaCl}\cdot\text{L}^{-1}$, after showing blood concentrations of $110\ \text{mmol NaCl}\cdot\text{L}^{-1}$, at the beginning of the experiments. In seawater solutions above 140 $\text{mmol}\cdot\text{L}^{-1}$, larvae and adults remained isotonic with the external media; the passive response expected from freshwater animals. In a later series of experiments, Morris (1972) carried out monthly assessments of ability to osmoregulate in individual metamorphosing brook lampreys in hypertonic solutions. Nine out of 20 were able to balance water in hypertonic (33%) seawater and two of these maintained their weight in 70% seawater. The monthly tests showed that seawater osmoregulatory ability was limited to a short period which started in November and ceased in January of the following year, after which those individuals which could marine-osmoregulate behaved like maturing adults when returned to freshwater and spawned in May or June of the same year. This implies that some of the dwarf forms have maintained the ability to osmoregulate in seawater and that this is a vestigial physiological mechanism which is normally unused.

The reasons for the variations in osmoregulatory behavior are uncertain, but there may be a transient phase during the development of the newly formed foregut which allows swallowing to occur in a few animals. Studies of the gill cells for possible changes would be very interesting in view of the changes which take place in the macropthalmia and feeding adults of other species (Pickering and Morris 1976; Youson and Freeman 1976).

The pattern of events of *L. fluviatilis* larvae follows that for *L. planeri* except that all macropthalmia stages seem to be able to survive in seawater (Potter and Huggins 1973; Pickering & Morris 1976).

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Anderson, W. C., and P. J. Manion. 1977. Morphological development of the integument of the sea lamprey, *Petromyzon marinus*. J. Fish. Res. Board Can. 34: 159–163.

Andrews, M. 1974. Fresh-water osmoregulation and its control in lampreys. Ph.D. thesis. Univ. Nottingham, Nottingham, UK.

Beamish, F. W. H. 1980. Osmoregulation in juvenile and adult lampreys. Can. J. Fish. Aquat. Sci. 37: 1739–1750.

Beamish, F. W. H., and I. C. Potter. 1972. Timing of changes in blood, morphology and behaviour of *Petromyzon marinus* during metamorphosis. J. Fish. Res. Board Can. 29: 1277–1282.

Beamish, F. W. H., P. D. Strachen, and E. Thomas. 1978. Osmotic and ionic performance of the anadromous sea lamprey, *Petromyzon marinus*. Comp. Biochem. Physiol. 60A: 435–443.

Black, V. S. 1957. Excretion and osmoregulation, p. 163–205. *In* M. Brown [ed.] The physiology of fishes. Academic Press, New York.

Bull, J. M., and R. Morris. 1967. Studies on freshwater osmoregulation in the ammocoete larva of *Lampetra planeri* (Bloch). 1. Ionic constituents, fluid compartments, ionic compartments and water balance. J. Exp. Biol. 47: 485–494.

Christie, R. M., and H. I. Battle. 1963. Histological effects of 3-trifluormethyl-4-nitrophenol (TFM) on larval lampreys and trout. Can. J. Zool. 41: 51–63.

Conway, E. J. 1945. The physiological significance of inorganic levels in the internal medium of animals. Biol. Rev. 20: 56–72.

Czopek, J., and O. Sawa. 1971. The structure and vascularisation of the skin and gills in the river lamprey (*Lampetra fluviatilis* L.) Acta Anat. 79: 305–320.

Dainty, J., and C. R. House. 1966. An examination of the evidence for membrane pores in frog skin. J. Physiol. (Lond). 185: 172–184.

Diem, K., and C. Lentner. [ed.] 1970. Scientific tables: Documenta Geigy. J. R. Geigy, S. A. Basle, Switzerland.

Downing, S. W., and R. R. Novales. 1971a. The fine structure of lamprey epidermis. 1. Introduction and mucous cells. J. Ultrastruct. Res. 35: 282–294.

1971b. The fine structure of lamprey epidermis. 2. Club cells. J. Ultrastruct. Res. 35: 295–303.

1971c. The fine structure of lamprey epidermis. 3. Granular cells. J. Ultrastruct. Res. 35: 304–313.

Fischer, G., and W. Albert. 1971. Ein biologisch wirksames Peptid aus der Haut von Neunaugen. Naturwissenschaften 58: 363.

Fontaine, M. 1930. Recherches sur le milieu intérieur de la lamproie marine (*Petromyzon marinus*). Ses variations en fonction de celles du milieu extérieur. C.R. Acad. Sci. Paris 191: 680–692.

1932. Sur la relation existant chez les poissons marins et potamotoques entre le teneur en phosphore inorganique du sérum et l'ossification du squellete. C.R. Acad. Sci. Paris 194: 395–396.

Gérard, P. 1954. Organes uro-génitaux, p. 977. *In* P. P. Grassé [ed.] Traité de zoologie. Vol 12. Masson, Paris.

Gordon, M. S. 1959. Ionic regulation in the brown trout (*Salmo trutta* L.) J. Exp. Biol. 36: 227–252.

Hardisty, M. W. 1956. Some aspects of osmoregulation in lampreys. J. Exp. Biol. 33: 431–437.

Hoar, W. S. 1966. General and comparative physiology. Prentice-Hall, Englewood Cliffs, NJ. p. 284.

Kaye, J. M. 1963. Fresh-water osmoregulation in ammocoete larvae (*Lampetra planeri*) (Bloch). Ph.D. thesis, Univ. Nottingham, Nottingham, UK.

Kerr, J. G. 1919. Textbook of embryology, Vol. II. Vertebrata with the exception of Mammalia. Macmillan, London. 221 p.

Kirschner, L. B. 1955. On the mechanism of active Na transport across frog skin. J. Cell. Comp. Physiol. 45: 61–88.

Krogh, A. 1937. Osmotic regulation in freshwater fishes by active absorption of chloride ions. Z. Vgl. Physiol. 24: 656–666.

Lewis, S. V. 1980. Respiration of lampreys. Can. J. Fish. Aquat. Sci. 37: 1711–1722.

Lewis, S. V., and I. C. Potter. 1976. Gill morphometrics of the lamprey, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). Acta. Zool. (Stockholm) 57: 103–122.

Litman, G. W., D. Frommel, J. Finstad, J. Howell, B. W. Pollara, and R. A. Good. 1970. The evolution of the immune response. VIII Structural studies of the lamprey immunoglobulin. J. Immunol. 105: 1278–1285.

Logan, A. G., R. J. Moriaty, and J. C. Rankin. 1980. A micropuncture study of kidney function in the river lamprey, *Lampetra fluviatilis*, adapted to fresh-water. J. Exp. Biol. 85: 137–147.

Marchalonis, J. J. 1977. Immunity in evolution. Edward Arnold, London. p. 73–78.

Marchalonis, J. J., and G. M. Edelman. 1968. Phylogenetic origins of antibody structure. 111. Antibodies in the primary immune response of the sea lamprey, *Petromyzon marinus*. J. Exp. Med. 127: 891–914.

Mathers, J. S., and F. W. H. Beamish. 1974. Changes in serum osmotic and ionic concentration in land-locked *Petromyzon Marinus*. Comp. Biochem. Physiol. 49A: 677–688.

Morris, R. 1956. The osmoregulatory ability of the lapern (*Lampetra fluviatilis* L.) in sea water during the course of its spawning migration. J. Exp. Biol. 33: 235–248.

1972. Osmoregulation, p. 193–239. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys, Vol. II. Academic Press, New York–London.

Morris, R., and J. M. Bull. 1968. Studies on freshwater osmoregulation in the ammocoete larva of *Lampetra planeri* (Bloch). 2. The effect of de-ionized water and temperature on sodium balance. J. Exp. Biol. 48: 597–609.

1970. Studies on freshwater osmoregulation in the ammocoete larva of *Lampetra planeri* (Bloch). 3. The effect of external and internal sodium concentration on sodium transport. J. Exp. Biol. 52: 275–290.

Morris, R., and D. S. Islam. 1969. The effect of hormones and hormone inhibitors on blood sugar regulation and the Follicles of Langerhans in ammocoete larvae. Genl. Comp. Endocrinol. 12: 81–90.

Morris, R., and A. D. Pickering. 1975. Ultrastructure of the presumed ion-transporting cells in the gills at ammocoete lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). Cell Tissue Res. 163: 327–341.

1976. Changes in the ultrastructure of the gills of the river lamprey, *Lampetra fluviatilis* (L.), during the anadromous spawning migration. Cell Tissue Res. 173: 271–277.

Nagano, H., K. Hosaka, and R. Shukuya. 1976. The fastest migrating component of lamprey serum in zone electrophoresis. Comp. Biochem. Physiol. 54B: 369–374.

Ooi, E. C., and J. H. Youson. 1976. Growth of the opisthonephric kidney during larval life in the anadromous sea lamprey, *Petromyzon marinus* L. Can. J. Zool. 54: 1449–1458.

Patinawin, S. 1967. Studies on tissues involved in fresh-water osmoregulation in ammocoete larvae (*Lampetra planeri* Bloch). Ph.D. thesis, Univ. Nottingham, Nottingham, UK.

Pelc, S. R., and T. C. Appleton. 1965. Distribution of tritiated thymidine in various tissues. Nature 205: 1287.

Pfeiffer, W., and T. F. Fletcher. 1964. Club cells and granular cells in the skin of the lamprey. J. Fish. Res. Board Can. 21: 1083–1088.

Pickering, A. D. 1973. The measurement of unidirectional sodium fluxes in the non-stressed ammocoete river lamprey, *Lampetra fluviatilis* L. Comp. Biochem. Physiol. 44A: 165–176.

Pickering, A. D., and R. Morris. 1970. Osmoregulation of *Lampetra fluviatilis* and *Petromyzon marinus* (Cyclostomata) in hypertonic solutions. J. Exp. Biol. 53: 231–243.

1976. Fine structure of the interplatelet area in the gills of the macrophthalmia stage of the river lamprey, *Lampetra fluviatilis* (L.). Cell Tissue Res. 168: 433–443.

Pietschmann, V. 1933. Cyclostomata. Handb. Zool. 6(1): 127–336.

Pollara, S., G. W. Litman, J. Finstad, J. Howell, and R. A. Good. 1970. The evolution of the immune response. VII Antibody to human "O" cells and properties of the immunoglobulin in lamprey. J. Immunol. 105: 738–745.

Potter, I. C., and F. W. H. Beamish. 1978. Changes in haematocrit and haemoglobin concentration during the life cycle of the anadromous sea lamprey *Petromyzon marinus* L. Comp. Biochem. Physiol. 60A: 431–434.

Potter, I. C., B. J. Hill, and S. Gentleman. 1970. Survival and behaviour of ammocoetes at low oxygen tensions. J. Exp. Biol. 53: 59–73.

Potter, I. C., and R. J. Huggins. 1973. Observations on the morphology, behaviour and salinity tolerance of downstream migrating river lampreys (*Lampetra fluviatilis*). J. Zool. Lond. 169: 365–379.

Potts, W. T. W., and G. Parry. 1964. Osmotic and ionic regulation in animals. Pergamon Press, London. 167 p.

Robertson, J. D. 1974. Osmotic and ionic regulation in cyclostomes, p. 149–193. *In* M. Florkin and B. T. Scheer [ed.] Chemical zoology, Vol. VIII. Academic Press, New York and London.

Sawyer, P. J. 1959. Effect of certain chemicals on mucus-producing cells of *Petromyzon marinas*. Trans. Am. Fish. Soc. 88: 305–309.

Sawyer, W. H. 1955. Data from V. S. Black 1957. Excretion and osmoregulation, p. 174. *In* M. E. Brown [ed.] The physiology of fishes, Vol. 1. Academic Press, NY.

Shaw, J. 1959. The absorption of sodium ions by the crayfish *Astacus palipes* Lereboullet. 1. The effect of external and internal sodium concentrations. J. Exp. Biol. 36: 126–144.

Sterba, G. 1953. Die Physiologie und Histogenese der Schilddrus und der Thymus beim Bachneunauge: als Grundlagen phylogenetischer Studien uber de Evolution der innersecretorischen Kiemendarmderivate. Wiss. Z. Friedrich-Schiller-Univ. Jena Math.-Naturwiss. Reihe 2: 239–298.

1961. Zur phylogenese des Kiemendarmes der Chordaen. Int. Rev. Gesamten Hydrobiol. Hydrogr. 46: 105–113.

Thomas, M. L. H., and H. R. McCrimmon. 1964. Variability in paper electrophoretic patterns of the serum of land-locked sea lamprey, *Petromyzon marinus* Linnaeus. J. Fish. Res. Board Can. 21: 239–246.

Thorson, T. B. 1959. Partitioning of body water in sea lamprey, Science, NY. 130: 99–100.

1961. The partitioning of body water in Osteichthyes. Photogenetic and ecological implications in aquatic vertebrates. Biol. Bull. Mar. Biol. Lab. (Woods Hole, Mass.) 120: 238–254.

Torrey, T. W. 1938. The absorption of colloidal carbon from the body cavity of ammocoetes. A study of the structure and function of the larval kidneys and blood forming tissues. J. Morphol. 63: 163–178.

Urist, M. R. 1963. The regulation of calcium and other ions in the serum of hagfish and lampreys. Ann. N.Y. Acad. Sci. 109: 294–311.

Urist, M. R., and K. A. van der Putte. 1967. Comparative biochemistry of the blood of fishes: identification of fishes by the chemical composition of serum, p. 271–285. *In* P. W. Gilbert, R. F. Matthewson, and D. P. Rall [ed.] Sharks, skates and rays. Johns Hopkins Press, Baltimore, MD.

Webster, R. O., and B. Pollara. 1969. Isolation and partial characterisation of transferrin in the sea lamprey, *Petromyzon marinus*. Comp. Biochem. Physiol. 30: 509–527.

Wheeler, W. M. 1899. The development of the urinogenital organs of the lamprey. Zool. Jahrb. Abt. Anat. Ontog. Tiere 13: 1–88.

Wikgren, B. J. 1953. Osmotic regulation in some aquatic animals with special reference to the influence of temperature. Acta Zool. Fenn. 71: 1–102.

Youson, J. H. 1970. Observations on the opisthonephric kidney of the sea lamprey of the Great Lakes, *Petromyzon marinus* L. at various stages during the life cycle. Can. J. Zool. 48: 1313–1316.

1980. Morphology and physiology of lamprey metamorphosis. Can. J. Fish. Aquat. Sci. 37: 1687–1710.

Youson, J. H., and P. A. Freeman. 1976. Morphology of the gills of larval and parasitic adult sea lamprey, *Petromyzon marinus* L. J. Morphol. 149: 73–103.

Youson, J. H., and D. B. McMillan. 1970a. The opisthonephric kidney of the sea lamprey of the Great Lakes. Part 1. The renal corpuscle. Am. J. Anat. 127: 207–232.

1970b. The opisthonephric kidney of the sea lamprey of the Great Lakes. Part 2. Neck and proximal segments of the tubular nephron. Am. J. Anat. 127: 233–257.

1971a. The opisthonephric kidney of the sea lamprey of the Great Lakes. Part 3. Intermediate, distal and collecting segments of the ammocoete. Am. J. Anat. 130: 55–71.

1971b. The opisthonephric kidney of the sea lamprey of the Great Lakes. Part 4. Intermediate distal and collecting segments of the adult. Am. J. Anat. 130: 281–303.

1971c. The opisthonephric kidney of the sea lamprey of the Great Lakes, *Petromyzon marinus* L. Part 5. The archinephric duct. Am. J. Anat. 131: 289–313.

1971d. Intertubular circulation in the opisthonephric kidneys of adult and larval sea lamprey, *Petromyzon marinus* L. Anat. Rec. 170: 401–411.

Evolution of the Brain–Pituitary Relationship: Evidence from the Agnatha[1]

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GORBMAN, A. 1980. Evolution of the brain–pituitary relationship: evidence from the Agnatha. Can. J. Fish. Aquat. Sci. 37: 1680–1686.

In the brain of the lamprey there are neurosecretory cells that manufacture and carry known hormonal materials to the neurohypophysis, which is that part of the diencephalic floor that is adjacent to the adenohypophysis. The adenohypophysis is differentiated into a pars distalis and a pars intermedia. However, unlike all other vertebrates, there is no vascular or nervous connection between the neurohypophysis and the pars distalis. If there is any regulation of the adenohypophysis by the hormones released from the endings of neurosecretory axones in the neurohypophysis, it would have to be by diffusion across the intervening connective tissue. Such regulation remains to be demonstrated.

It is difficult to decide whether this relationship between neurohypophysis and pars distalis in the lamprey (and hagfish) is primitive or degenerate in its evolution. However, in three groups of more primitive fishes an intermediate condition is found in which a vascular connection exists between the neurohypophysis and a part of the adenohypophysis. This being so, we may speculate that the lamprey and other cyclostomes represent the simplest and most primitive anatomical relationship between brain and adenohypophysis, one in which the two organs are merely apposed, allowing neurosecretions to diffuse between the two. In the elasmobranchs, holocephalians, and the coelacanth, part of the pars distalis has been vascularized by portal vessels beginning in the neurohypophysis. In all other vertebrates the entire pars distalis is so vascularized.

Key words: brain, pituitary gland, neurosecretion, hormones, evolution, *Lampetra richardsoni*, *L. tridentata*, *Petromyzon marinus*

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Il y a dans le cerveau de la lamproie des cellules neurosécrétrices qui produisent et transportent des matières hormonales connues à la neurhypophyse, cette partie du plancher du diencéphale adjacente à l'adénohypophyse. L'adénohypophyse se subdivise en une pars distalis et une pars intermedia. Cependant, contrairement à tous les autres vertébrés, il n'y a pas de liaison vasculaire ou neurale entre la neurhypophyse et la pars distalis. Tout contrôle, s'il en existe un, de l'adénohypophyse par les hormones libérées de l'extrémité des axones neurosécréteurs dans la neurhypophyse devrait se faire par diffusion à travers le tissu conjonctif intermédiaire. Un tel contrôle est encore à démontrer.

On n'est pas sûr si cette relation entre la neurhypophyse et la pars distalis chez la lamproie (et le myxine) est primitive ou dégénérée dans son évolution. Cependant, on observe chez trois groupes de poissons primitifs une condition intermédiaire selon laquelle il y a liaison vasculaire entre la neurhypophyse et une partie de l'adénohypophyse. Dans ce cas, il est permis de supposer que la lamproie et autres cyclostomes représentent la relation anatomique la plus simple et la plus primitive entre le cerveau et l'adénohypophyse, relation selon laquelle les deux organes sont simplement apposés, permettant une diffusion des neurosécrétions entre les deux. Chez les élasmobranches, les holocéphales et le coelacanthe, une portion de la pars distalis est vascularisée par des vaisseaux portes ayant leur origine dans la neurhypophyse. Chez tous les autres vertébrés, le pars distalis entière est vascularisée de cette manière.

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THE concept of the vertebrate brain as an endocrine organ originated in the 1930's, when Scharrer proposed, on morphological grounds, the possibility that the hormones of the neurohypophysis are actually formed in hypothalamic nerve cells (Scharrer 1979). This concept has been broadened and greatly enriched in detail through the studies of many workers in the new field of neuroendocrinology, but mostly such studies have dealt with mammals and birds.

Essentially, the endocrine functions of the vertebrate brain involve the synthesis of a variety of peptide hormones in the perikarya of cells in the diencephalon, conduction of these substances along axonal tracts leading to the neurohypophysis, and release (or "secretion") of these substances into blood capillaries in the neurohypophysis. Neurosecretion in the neurohypophysis is of two general types. In one (pars nervosa), the neurosecretory axonal endings are upon blood capillaries that lead directly into the systemic veins and the heart for immediate general distribution. In the other type, the secretory nerve cells end upon capillaries (in the median eminence) which lead into small portal veins that proceed to the pars distalis, and there break up into a secondary capillary network. It is generally agreed that the function of this latter median eminence to pars distalis system is to regulate secretion of the six pars distalis hormones through action of "releasing hormones" from the brain.

The neurosecretory perikarya in the hypothalamus are innervated through aminergic, cholinergic, and still other kinds of synaptic relationships with afferents from a variety of sources. Thus, the hypothalamic neurosecretory system forms an essential link in the variety of hormone-mediated responses the organism makes to sensory-perceived physical stimuli from the environment (photic, optic, auditory, tactile, thermal, etc.). As such, the hypothalamo–hypophysial neurosecretory system must play a key role in the adaptive evolution of the vertebrates. Indeed, many studies already have shown how this system is involved in the intricate regulation of environmentally cued features in reproductive, metabolic, behavioral (e.g. migration, estivation), developmental, thermoregulatory, and other basic functions.

Since the brain–pituitary relationship is so fundamental among the vertebrate adaptive mechanisms, it is of particular interest to understand its properties in the Agnatha, the living vertebrates whose origin is from the most primitive sources in the evolutionary line. This review, while focussing upon information from our own studies with lampreys, will outline other current information available at this time. It will summarize what we know of the development, morphology, and functional properties of the agnathan brain–pituitary relationship and attempt to interpret the evolution of this relationship from such information.

DEVELOPMENT OF THE LAMPREY PITUITARY GLAND

The final topographic disposition of the epithelial (adenohypophysial) and nervous (neurohypophysial) tissues in lampreys is generally similar to that in higher vertebrates (Fig. 1). That is, the neurohypophysis and adenohypophysis are apposed to each other in an anteroposterior direction. However, the development of this anatomic relationship in lampreys differs in several important aspects from other vertebrates.

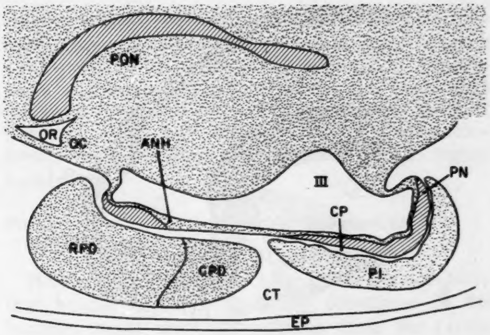

FIG. 1. Relationships of the hypothalamo–hypophysial structures of *Lampetra tridentata* as they would appear in a sagittal section. Areas in which aldehyde-fuchsin staining perikarya or axonal terminals are located are indicated by oblique lines. The pars distalis (RPD and CPD) is coextensive with the anterior neurohypophysis ANH, separated by a connective tissue sheet. The pars intermedia PI is applied to the posterior neurohypophysis, or pars nervosa PN, separated from it by a plexus of blood vessels (see also Fig. 4), CP. Other labels: EP, mucosa of nasohypophysial canal; CT, connective tissue; CPD, caudal pars distalis; OC, optic chiasm; OR, preoptic recess; PON, preoptic nucleus; RPD, rostral pars distalis; III, third ventricle.

There has been no recent study of the development of the lamprey pituitary gland, but older work has been summarized by Ziegler (1921) and more recently by Wingstrand (1966) (Fig. 2, 3). The adenohypophysis is derived in the lamprey embryo as a posterior projection from a single median epithelial pit (olfactory pit) on the front of the embryonic head. This adenohypophysial anlage extends toward, and makes contact with, the infundibulum, the future neurohypophysis. The olfactory opening rotates dorsad as the lip of the oral cavity becomes larger, growing between the nasal opening and the mouth. Thus, the single median olfactory organ develops from part of the original anlage, and the adenohypophysis more posteriorly from the same anlage.

This pattern of development is reminiscent of the amphibian embryo, in which the adenohypophysis forms as a finger of tissue growing inward from the front of the head, between the paired olfactory pits, which remain lateral to the adenohypophysial rudiment. In virtually all other vertebrates (excepting teleosts) the adenohypophysis forms from the oral ectoderm when a strong flexion of the embryonic head

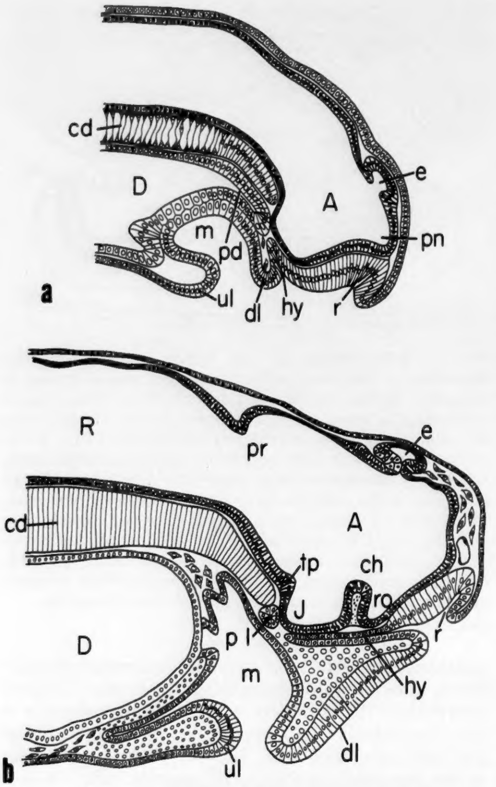

FIG. 2. Schematic sagittal sections through the heads of embryos of the lamprey *Petromyzon marinus*. (a) represents an embryo of 3 mm. At this stage an elongated nasohypophysial pit has formed on the ventral side of the head, against the forebrain. This pit has an anterior extension, r, the future olfactory organ, and a posterior extension, hy, which will form the adenohypophysis. The hypophysial rudiment is separated from the mouth m, by an upper lip, dl. Other abbreviations: A, forebrain; D, pharynx; cd, notochord; e, pineal; pd, preoral gut; ul, lower lip. The lower figure (b) represents a slightly older embryo of 4 mm. At this stage the nasohypophysial pit has mostly closed over, leaving a single median opening that is now anterior, and in Fig. 3 will be seen to become dorsal, mostly because of growth of the upper lip dl. A small structure, pl, has broken off of the tip of the hypophysial rudiment. This was shown later by Leach (1951) to be the precociously detached future pars intermedia. Abbreviations as in (a) with the addition of the following: J, infundibulum of the diencephalon; R, rhombencephalon; ch, chiasma; ro, preoptic recess; tp, tuberculum posterior. (Adapted from Kupffer (1906).)

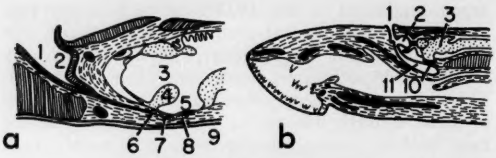

FIG. 3. (a) Sagittal section of the dorsal part of the head of an older ammocoete larva of *Petromyzon*. The opening of the nasohypophysial pit (1) is dorsal, separated from the mouth by the dorsal lip (all of the tissue to the left). The olfactory organ (2) is forming anterior to the brain (3). The optic chiasma (4) roughly divides the foreshortened telencephalon from the diencephalon. The neurohypophysis (5) is shown as black. The adenohypophysis is still attached by a long epithelial stalk to the olfactory organ, reflecting its early origin. The parts of the adenohypophysis shown are the rostral pars distalis (6), the caudal pars distalis (7), and the pars intermedia (8). The epithelium (9) of the mucosa of the nasohypophysial duct (11) lies below the adenohypophysis. (b) Sagittal section of the head of an adult *Petromyzon* to show the definitive positions and relative sizes of some of the structures shown for the ammocoete in (a). Label numbers are the same as in (a) except that 10 is the adenohypophysis. Figures have been modified slightly from K. G. Wingstrand (1966).

forms a wedge-shaped space between the head and the heart region. Thus, in summary, the lamprey adenohypophysis is a derivative of the definitive ectoderm at the top of the head; in amphibians it is derived from ectoderm that is later near the anterior tip of the head, between the nostrils; in all other vertebrates it is a derivative of ectoderm that is part of the definitive mouth. However, it must be indicative of some kind of phylogenetic conservatism and eventual functional significance, that in all vertebrates, including the lamprey, the adenohypophysial rudiment very early grows toward the infundibular part of the brain and further differentiates in that position.

It is unfortunate that there is no information concerning the development of the myxinoid brain–pituitary relationship. Such information might enlighten us concerning the typical or possibly specialized character of adenohypophysial ontogeny in lampreys.

MORPHOLOGICAL BASES FOR COMMUNICATION BETWEEN NEUROHYPOPHYSIS AND ADENOHYPOPHYSIS OF LAMPREYS

We must assume at this point that the coextensiveness and contiguity of the adenohypophysis and the neurohypophysial part of the brain evolved because of some functional value that this relationship confers. In higher vertebrates this functional value seemingly lies in the linkage of control of adenohypophysial secretions to sensory and other nervous events. The anatomical basis for exertion of such functional control by the brains of higher vertebrates is by two means: vascular and nervous. That is, in many vertebrates there is a vascular connection, beginning in the median eminence

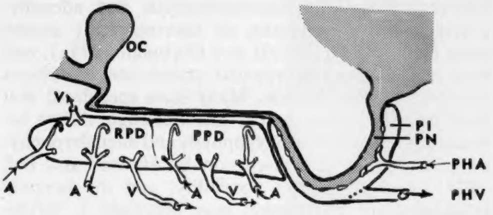

FIG. 4. Diagrammatic representation of the vascular supply to the adenohypophysis of *Petromyzon marinus*, projected onto a sagittal section. Dotted area represents the brain and neurohypophysis. The pars distalis is supplied by a series of small arteries (A) and arterioles from the internal carotid artery that enter the gland from the ventral side; near the dorsal edge of the gland they turn as a series of loops and exist as venules (v) from the gland. Between the pars nervosa (PN) and pars intermedia (PI), on the other hand a single posterior hypophysial artery penetrates from the posterior direction and breaks up into a capillary network between the PN and PI. This network drains into the posterior hypophysial vein, PHV. There is no vascular connection between the anterior neurohypophysis and the pars distalis. Other abbreviations: OC, optic chiasma; PPD, proximal or caudal pars distalis; RPD, rostral pars distalis. (From A. Gorbman (1965).)

and terminating in the pars distalis. The pars intermedia generally has no such vascular relationship to the brain, but in most vertebrate groups, pars intermedia cells are innervated directly by neurones that enter it through the pars nervosa. Only in teleosts, apparently, are glandular cells of the pars distalis directly innervated by hypothalamic neurosecretory neurones (Vollrath 1972; Holmes and Ball 1974).

Study of vascular patterns revealed by India ink injections in lampreys (*Petromyzon*) by Jasinski (1969) and Gorbman (1965) revealed a pattern that is different from all other vertebrates. That is, the pars distalis is well vascularized by arterial loops that enter and leave each lobule of glandular tissue from the ventral side, the side which is away from the neighboring neurohypophysis (Fig. 4). There are very few small vessels connecting the pars distalis with the brain, and these appear to be venous, moving blood in the direction from the pars distalis toward larger veins. Thus a portal connection from the neurohypophysis to the pars distalis is lacking, or at best extremely poorly developed. Between the pars intermedia and the pars nervosa of *Petromyzon*, on the other hand, there is a plexus of capillaries. However, these vessels do not enter the pars intermedia, but rather drain into a relatively large vein conducting blood away from the hypophysial region. Thus, in contrast to all other vertebrates, in *Petromyzon* there appears to be no anatomic means for irrigating the pars distalis with blood containing possible neurosecretory materials from the brain.

The question of possible direct innervation of the lamprey adenohypophysis by neurones from the neurohypophysis was approached by Tsuneki and Gorbman (1975a, b) by use of electron microscopy. No evidence was found of such innervation. This leaves open the general question of how or whether the brain of lampreys exerts any kind of control over adenohypophysial function, as it does in all higher vertebrates.

PRESENCE OF HYPOPHYSIOTROPIC SUBSTANCES IN THE LAMPREY BRAIN

Holmes and Ball (1974) have raised the possibility that hypophysiotropic regulating substances in the lamprey might move by diffusion from the neurohypophysis to the adjacent pars distalis. Thus, this part of the neurohypophysis might be a primitive "prevascular" type of median eminence. It must be shown, however, whether or not hypophysiotropic substances exist in the lamprey. Fortunately, some data in this connection already have appeared. Jackson and Reichlin (1974), for example, have found immunoreactive thyrotrophin releasing hormone (TRH) in extracts of whole brain of larval lampreys.

Crim et al. (1979a, b), using an antibody prepared against synthetic decapeptide gonadotropin releasing hormone (LHRH), and an immunocytochemical procedure, showed that LHRH is demonstrable in cells of the preoptic nucleus of the pacific lamprey, *Lampetra tridentata* (Fig. 5), and the western brook lamprey, *Lampetra richardsoni*. Furthermore, in the preoptic nuclei of *L. richardsoni* there was evidence of considerably more LHRH activity in sexually maturing specimens than in younger ammocoetes (Fig. 6); in sexually maturing metamorphosing animals, the number of cells containing LHRH activity was larger. LHRH activity was visible in axons, which were more or less gathered as a tract extending into the neurohypophysis. It is interesting that immunocytochemical staining of LHRH was limited to the preoptic nuclear area. Similar procedures applied to hagfish brains by Crim et al. (1979a) failed to reveal any LHRH activity.

Immunoreactive growth hormone release-inhibiting hormone (SRIF) has been found in extracts of hagfish brain, but tests for this substance have not been made in lampreys (Crim et al. 1978). Furthermore, no studies yet have been reported concerning corticotropin- or prolactin-releasing hormonal activity in agnathan brains.

General Discussion

In sum, the study of hypothalamo–hypophysial relationships in the petromyzontids appears to have created more questions than have been answered (Larsen 1969). From the recent work of Crim et al. (1979a, b), for example, it would appear that LHRH in lampreys is synthesized in certain preoptic nuclear perikarya, and delivered via axonal tracts to the neurohypophysis. However, there is a connective tissue

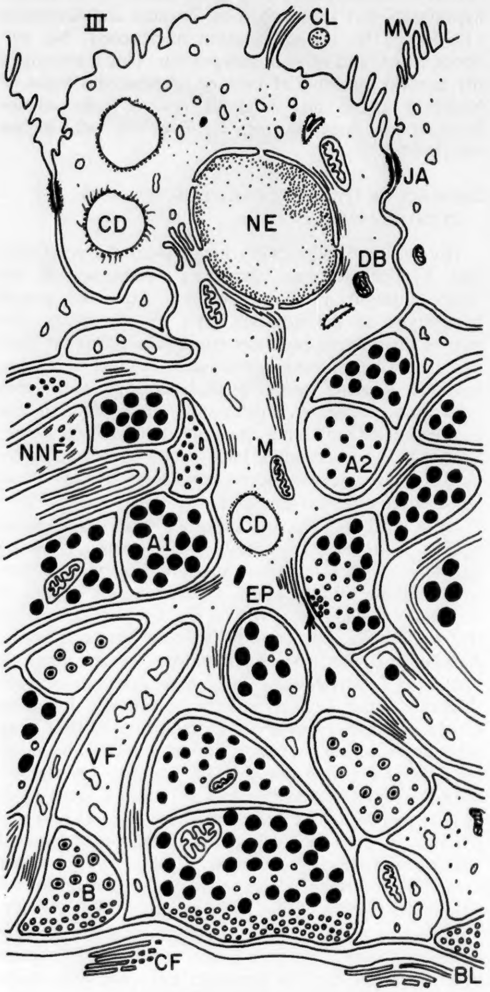

FIG. 5. Schematic summary of the ultrastructure of the anterior neurohypophysis of *Lampetra tridentata*. The number of axons and ependymal cells, as shown, is much less than actual for clarity. Ciliated (CL) ependymal cells (NE) extend from the ventricular border (III) to the basal lamina (BL) connective tissue of connective tissue fibers (CF) that separates the neurohypophysis from the adenohypophysis below. At this level this connective tissue septum is about 25 μm thick. The region contains a variety of neurosecretory axons and endings. At least two types of peptidergic nerve fibers and endings containing characteristic granules (A1, A2) can be recognized and one type of "dense core" granule containing nerve fiber is seen (B). Occasional synaptoid structures were seen at some of the nerve endings (at arrow). The endings of some of the neurosecretory cells at the connective tissue septum have led some authors (see text) to speculate that neurosecretory materials released here could diffuse to the adjacent pars distalis. Other abbreviations: CD, colloid droplet; DB, dense body; EP, ependymal process; JA, junctional apparatus; M, mitochondrion; NNF, nonneurosecretory fiber; VF, vesicular formation. (From Tsuneki and Gorbman 1975a.)

barrier between the neurohypophysis and adenohypophysis and pars distalis; no neurosecretory axones cross this barrier (Tsuneki and Gorbman 1975a), and existence of a portal vascular connection is dubious (Gorbman 1965) at best. Many have speculated that hypothalamic neurosecretory material might diffuse between the anterior neurohypophysis and adenohypophysis of lampreys (see discussion by Holmes and Ball 1974). This remains a possibility, and the lamprey brain–pituitary relationship may represent a "primitive" type of "premedian eminence," but it appears unlikely. If diffusion of hypothalamic neurosecretory material were a factor in control of secretion of pars distalis hormones, it would affect only the tops of the columns of cells of the pars distalis. It would seem that more ventrally located cells of the lamprey pars distalis would not receive such putative diffused material since this material would be absorbed in the capillary loops of this region, and carried away before diffusing very far, or reduced to ineffective concentrations.

Comparisons can be made with the situation in myxinoids, where again, in pacific hagfish, *Eptatretus stouti*, there is no nervous connection between neurohypophysis and adenohypophysis, and a vascular connection is very questionable. However, in *E. burgeri*, which has a seasonally limited breeding period (in contrast to the seemingly uncontrolled breeding of *E. stouti*), Kobayashi and Uemura (1972) claim that there is a median eminence-like structure with up to 20 putative portal vessels between the neurohypophysis and adenohypophysis. The direction of flow of blood in these vessels remains to be clarified, however.

It should be emphasized that in lampreys, whether permanently stream-dwellers, or anadromous migratory species, there is a seasonally limited reproductive period. Thus, there is a need for linkage of gonadotropic activity to seasonal environmental cues. Such a linkage is provided by the hypothalamo–hypophysial neurosecretory system in other vertebrates. It is only partly represented in lampreys by the demonstrated presence of LHRH in certain hypothalamic neurones and fiber tracts terminating in the neurohypophysis (Crim et al. 1979a, b). In sexually active adult hagfish e.g. *E. stouti*, no hypothalamic LHRH is demonstrable by the same technique, and this hagfish which lives in constant darkness and at a constant temperature breeds continually, with no apparent gonadotropic control (see Matty et al. 1976).

Since there is little or no vascular or nervous com-

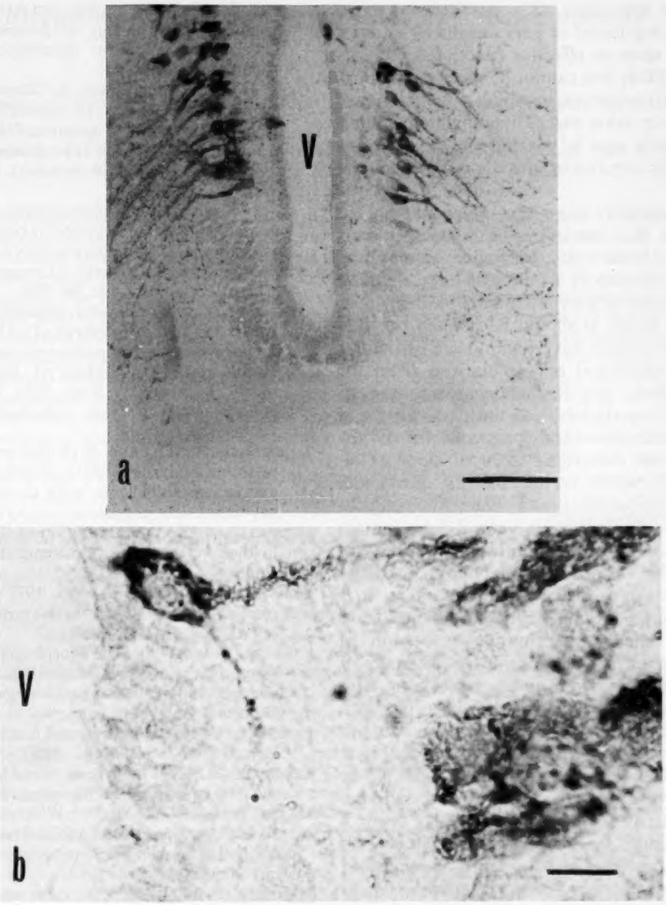

FIG. 6. (a) Low power photomicrograph of preoptic area of the hypothalamus of a reproductive western brook lamprey, *Lampetra richardsoni*. The only stain in this section is from the black reaction production after use of an immunohistochemical stain involving an antibody to synthetic decapeptide LHRH. The stain is contained not only in certain perikarya in the preoptic nucleus, but also can be traced through fiber tracts that extend into the neurohypophysis. V is the third ventricle of the brain. Scale bar, 50 μm. (b) Higher power photograph to show stained perikarya and a branched axon. Scale bar, 10 μm. These photographs were provided from research by Prof. J. W. Crim, Department of Zoology, University of Georgia, Athens, Georgia.

munication between the neurohypophysis and adenohypophysis of lampreys or hagfish, we may speculate concerning the stage of evolution of the median eminence represented by this condition. There are several alternative possibilities. First, it is conceivable that the agnathan brain–pituitary anatomical relationship represents an evolutionary regression from an earlier better developed median eminence like that seen in all other modern fish groups. The current agnathans have evolved during the period that was required for evolution of all other differentiated vertebrate groups, so that ample time for such regressive evolution has been available. Second, it is possible that diffusion of hypophysiotropic substances across the thin connective tissue septum between neurohypophysis and pars distalis is adequate. For regulation of pars intermedia function the close apposition with pars nervosa might be adequate. For regulation of pars distalis by anterior neurohypophysis, such an effective functional relationship appears less likely but cannot be ruled out. Third, it is possible that in lampreys, in which seasonally cued reproductive activity takes place, hypothalamic control over the pars distalis may be exerted via the secretion of hypophysiotropic substances into the general circulation.

If the latter possibility were real we would be left with the paradox that control of the lamprey pars distalis by the brain via systemic blood-borne hypophysiotropic substances would not have required the complex evolution of a hypothalamo–pituitary contiguity in the first place. It should be pointed out that several of the lower fishes have pars distalis structures that are neither innervated or vascularized from the brain. These include the Rechendachhypophyse of Holocephali, the "ventral lobe" of the pars distalis of elasmobranchs, and the distal pars distalis of the coelacanth *Latimeria*. According to J. M. Dodd (University College of North Wales. Bangor, Gwynedd, U.K., personal communication) the Rachendachhypophyse and the elasmobranch ventral lobe contain considerable quantities of gonadotrophin and thyrotrophin. Among the various neurohypophysial–adenohypophysial relationships discussed to this point, it is possible to conceive among them an evolutionary progression. (1) The most primitive expression of brain to adenohypophysis relationships is intimacy of association of pars intermedia and pars nervosa, with the pars distalis possibly regulated by diffusion from the anterior neurohypophysis, or via peripheral vascular control (petromyzontids). (2) In an intermediate phase the pars intermedia is even more intimately bound up with the pars nervosa; a part of the pars distalis becomes vascularized by a portal blood supply from a well-developed median eminence, while another part of the pars distalis remains independently vascularized (holocephalians, elasmobranchs, coelacanth). (3) In all other vertebrates, the pars intermedia (when present)–pars nervosa relationship essentially remains the same, and the entire pars distalis is irrigated by a portal system from the median eminence.

Like most phylogenetic speculation, the above scheme really cannot be proven. However, it has the advantage of consistency. That is, the most primitive brain–pituitary relationship is that in the lampreys; the intermediate anatomic relationship is found in several of the most primitive groups of fishes; the most complete median eminential portal control of the pars distalis is found in the more advanced vertebrates, the amphibians, reptiles, birds, and mammals. The teleosts in this scheme would represent another line of evolution from the agnathan base in which complete and direct invasion of the adenohypophysis by neurohypophysis become an alternative to development of a median eminence. However, it would seem that the teleosts probably evolved from forms that already had a well-developed median eminence.

CRIM, J. W., W. W. DICKHOFF, AND A. GORBMAN. 1978. Comparative endocrinology of piscine hypothalamic hypophysiotropic peptides: distribution and activity. Am. Zool. 18: 411–424.

CRIM, J. W., A. URANO, AND A. GORBMAN. 1979a. Immunocytochemical studies of luteinizing hormone-releasing hormone in brains of agnathan fishes. I. Comparisons of adult Pacific lamprey (*Entosphenus tridentata*) and the Pacific hagfish (*Eptatretus stouti*). Gen. Comp. Endocrinol. 38: 204–305.

1979b. Immunocytochemical studies of luteinizing hormone-releasing hormone in brains of agnathan fishes. II. Patterns of immunoreactivity in larval and maturing Western brook lamprey (*Lampetra richardsoni*). Gen. Comp. Endocrinol. 38: 290–299.

GORBMAN, A. 1965. Vascular relations between neurohypophysis and adenohypophysis of cyclostomes and the problem of evolution of hypothalamic neuroendocrine control. Arch. Anat. Micros. Morphol. Exp. 54: 163–194.

HOLMES, R. L., AND J. N. BALL. 1974. The pituitary gland. A comprehensive account. Cambridge University Press, Cambridge.

JACKSON, I. M. D., AND S. REICHLIN. 1974. Thyrotropin-releasing hormone (TRG): distribution in hypothalamic and extrahypothalamic brain tissues of mammalian and submammalian chordates. Endocrinology 95: 854–862.

JASINSKI, A. 1969. Vascularization of the hypophyseal region in lower vertebrates (cyclostomes and fishes). Gen. Comp. Endocrinol. Suppl. 2: 510–521.

KOBAYASHI, H., AND C. UEMURA. 1972. The neurohypophysis of the hagfish, *Eptatretus burgeri*. Gen. Comp. Endocrinol. Suppl. 3: 114–124.

KUPFFER, K. VON. 1906. Die Morphogenie des Centralnervensystems. *In* O. Hertwig [ed.] Handbuch der vergleichenden und experimentellen Entwicklungslehre der Wirbeltiere. Gustav Fischer, Jena.

LARSEN, L. O. 1969. Hypophyseal function in lampreys. Gen. Comp. Endocrinol. Suppl. 2: 522–527.

LEACH, W. J. 1951. The hypophysis of lampreys in relation to the nasal apparatus. J. Morphol. 89: 217–255.

MATTY, A. J., K. TSUNEKI, W. W. DICKHOFF, AND A. GORBMAN. 1976. Thyroid and gonadal function in hypophysectomized hagfish, *Eptatretus stouti*. Gen. Comp. Endocrinol. 30: 500–516.

SCHARRER, B. 1979. Neurosecretion and neuroendocrinology in historical perspective. *In* C. H. Li [ed.] Hormonal proteins and peptides, Vol. VI, Hypothalamic hormones. Academic Press, New York.

TSUNEKI, K., AND A. GORBMAN. 1975a. Ultrastructure of the anterior neurohypophysis and pars distalis of the lamprey, *Lampetra tridentata*. Gen. Comp. Endocrinol. 25: 487–508.

1975b. Ultrastructure of pars nervosa and pars intermedia of the lamprey, *Lampetra tridentata*. Cell Tissue Res. 157: 165–184.

VOLLRATH, L. 1972. Morphological correlates of releasing factors in the pituitary of the eel, *Anguilla anguilla*. *In* K. M. Knigge, D. E. Scott, and A. Weindl [ed.] Brain-endocrine interaction. Median eminence structure and function. S. Karger, Basel.

WINGSTRAND, K. G. 1966. Comparative anatomy and evolution of the hypophysis. *In* G. W. Harris and B. T. Donovan [ed.] The pituitary. Butterworths, London.

ZIEGLER, H. E. 1921. Lehrbuch der vergleichenden Entwicklungsgeschichte. Gustav Fischer, Jena.

Morphology and Physiology of Lamprey Metamorphosis[1]

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YOUSON, J. H. 1980. Morphology and physiology of lamprey metamorphosis. Can. J. Fish. Aquat. Sci. 37: 1687–1710.

Metamorphosis is highly synchronized in both landlocked and anadromous sea lampreys, *Petromyzon marinus*, and can be divided into seven clearly defined stages. Although there may be some subtle internal changes several months before the beginning of external metamorphosis, most internal and external changes are initiated simultaneously in early July in *P. marinus*. The time and degree to which various external anatomical features take place does not differ to any large degree in landlocked and anadromous sea lampreys. Observations on *P. marinus* and other lamprey species shows that variations in the time of completion of transformation or development of organs reflect the immediate needs of the animal. For example, transformation of the liver and development of the kidneys occur very early (stage 4) whereas organs and tissues involved in osmoregulation, feeding, and digestion do not reach their definitive adult condition until later stages. All organ systems seem to undergo some morphological transformation during metamorphosis. After the beginning of metamorphosis lipid is utilized as the primary source of energy during the nontrophic period which may last up to 10 mo. Physiological modifications accompanying the initiation of metamorphosis include changes in rate of oxygen consumption, in serum osmolarity and thyroxine levels, in the biochemistry of the blood, and in aspects of intermediary metabolism. There is no definitive information as to the factor(s) which control the metamorphic process in lampreys.

Key words: lampreys, metamorphosis, morphology, physiology

YOUSON, J. H. 1980. Morphology and physiology of lamprey metamorphosis. Can. J. Fish. Aquat. Sci. 37: 1687–1710.

Chez la grande lamproie marine, *Petromyzon marinus*, tant confinée en eau douce qu'anadrome, la métamorphose est hautement synchronisée et peut être divisée en sept stades clairement définis. Bien que de subtiles changements internes puissent se produire plusieurs mois avant le début de la métamorphose externe, la plupart des changements internes et externes débutent simultanément début juillet chez *P. marinus*. L'époque et le degré auxquels les diverses caractéristiques anatomiques s'établissent ne diffèrent pas beaucoup chez les lamproies confinées en eau douce et les lamproies anadromes. Des observations sur *P. marinus* et autres espèces de lamproies montrent une relation entre les variations de la fin de la transformation ou du développement des organes et les besoins immédiats de l'animal. Par exemple, le foie se transforme et les reins se développent assez tôt (stade 4), alors que les organes et les tissus impliqués dans l'osmorégulation, l'alimentation et la digestion n'atteignent que plus tard leur état adulte définitif. Tous les systèmes d'organes semblent subir quelque transformation morphologique lors de la métamorphose. Après le début de cette dernière, les lipides sont utilisés comme source première d'énergie durant la période non trophique qui peut durer jusqu'à 10 mois. Parmi les modifications physiologiques accompagnant le début de la métamorphose, on note les changements suivants : taux de consommation d'oxygène, osmolarité du sérum et niveaux de thyroxine, biochimie du sang et certains aspects du métabolisme intermédiaire. On ne connaît pas de façon définitive les facteurs contrôlant le processus de la métamorphose chez les lamproies.

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METAMORPHOSIS is a period in which an organism passes from one form or shape into another. This change in form usually occurs as a consequence of a variety of developmental processes taking place in the organism. In some cases, however, metamorphosis is a requirement to prepare organisms for life in a new habitat; that is "true metamorphosis" in the sense of Wald (1958). In this context, transformation of larval lampreys into adults is an example of true vertebrate metamorphosis. However, a number of species of lampreys do not feed or occupy a new habitat after meta-

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TABLE 1. Stages (1–7) in the metamorphosis of the anadromous sea lamprey (Youson and Potter 1979) and equivalent stages in the description in the landlocked form by Manion and Stauffer (1970).

Population	Mid-July	Mid- to late July	Mid-July to mid-Aug.	Late July to late Aug.	Mid-Aug. to early September	Mid-Aug. to mid-September	Sept., Oct., early Nov.	Dec. to June
Anadromous	1	2	3	4	5	6	7	Newly metamorphosed
Landlocked			1	2	3	4		5

morphosis. Despite this, the somatic changes undergone during the metamorphosis of nonparasitic species parallels those exhibited by parasitic species.

Müller (1856) recognized the relationship between larvae and adult lampreys when he observed an intermediate stage which he followed through to a young adult. From external pigmentation, narrowing of the mouth, and fusion of the transverse and lateral lips, reduction in oral papillae and cirri, modifications to the branchial region, and the appearance of horny projections (teeth) in the oral cavity, he concluded that the members of what were previously placed in the genus *Ammocoetes* were the larvae of lampreys. Siebold (1863) described seven stages during transformation of larval *Lampetra planeri*, and Kaensche (1890) and Bujor (1890, 1891a, b, c, d, e) gave the first extensive accounts of internal changes in the same species. Later, Balabai (1948) described 12 stages (including the ammocoetes and the adults) of *Eudontomyzon mariae*. More recently, descriptions have been provided of metamorphosis in *L. planeri* (Lohnisky 1967; Bird and Potter 1979a, b), *Lampetra fluviatilis* (Bird and Potter 1979a, b), *Lampetra japonica kessleri* (Poltorykhina 1971), and landlocked (Manion and Stauffer 1970) and anadromous (Potter et al. 1978b; Youson and Potter 1979) *Petromyzon marinus*.

It is clear from the very first investigations of the process that lamprey metamorphosis is a highly programmed and synchronized event. This paper attempts to consolidate the information provided in earlier and more recent studies on the morphological and physiological aspects of this interesting biological phenomenon. Particular emphasis is placed on results of a recent examination of metamorphosing specimens of the anadromous sea lamprey, *P. marinus*, collected in New Brunswick.

Staging

An important prerequisite for the study of lamprey metamorphosis is a clearly defined sequence of stages based on external features. Following the recognition by Müller (1856) that lampreys undergo specific phases or intervals in their metamorphic process, Siebold (1863) provided a staging of metamorphosis in *L. planeri*. Most descriptions of the metamorphic process monitor the structural changes in the eye, in the oral aperture, and in the coloration of the body and follow the development of the tongue-like piston, the teeth, and the dorsal fins. Metamorphosis in *P. marinus* was first described in detail by Manion and Stauffer (1970), who recognized four (1–4) transforming stages and a newly metamorphosed stage (often referred to as stage 5). When these stages were applied to anadromous *P. marinus* from New Brunswick it became evident that staging criteria should also include the timing of morphological events in all systems, including the internal organs. Some internal changes take place well before the onset of external metamorphosis, namely in the adenohypophysis (Thompson 1971) and in the nasohypophysial apparatus and accessory olfactory organs (Leach 1951). However, Youson et al. (1977) reported that modifications to many internal organs occur only a few weeks before the first sign of metamorphosis as described by Manion and Stauffer (1970) in their stage 1. As it is essential to be able to detect the earliest events in metamorphosis in any ontological and physiological study, the stages of metamorphosis in anadromous *P. marinus* were described (Youson and Potter 1979). There is no reason to doubt that such stages (Fig. 1) may also be applied to landlocked *P. marinus*. Moreover, relatively similar stages are present in *L. fluviatilis* and *L. planeri* located in European waters (Bird and Potter 1979a, b).

Since a comprehensive description of these stages in anadromous *P. marinus* is provided in Youson and Potter (1979), only a brief summary is provided here. The seven (1–7) stages of transforming individuals are compared with the four stages of Manion and Stauffer (1970) in Table 1. Such a comparison is possible because of the remarkable synchrony of metamorphosis in the two forms of *P. marinus* from year to year. Stage 1 in the anadromous form is marked by the appearance of the lateral eyes as small irregularly shaped grey patches of larger diameter than those of ammocoetes. That this is the beginning of metamorphosis is further substantiated by consistent, subtle changes in many internal organs which are revealed during microscopic examination. Stage 2 is more clearly defined with a round eye and prominent papilla-like projections on the inner dorsal surface of the oral hood. Stages 3, 4, and 5 are similar to stages 1, 2, and 3, respectively, of Manion and Stauffer (1970); major

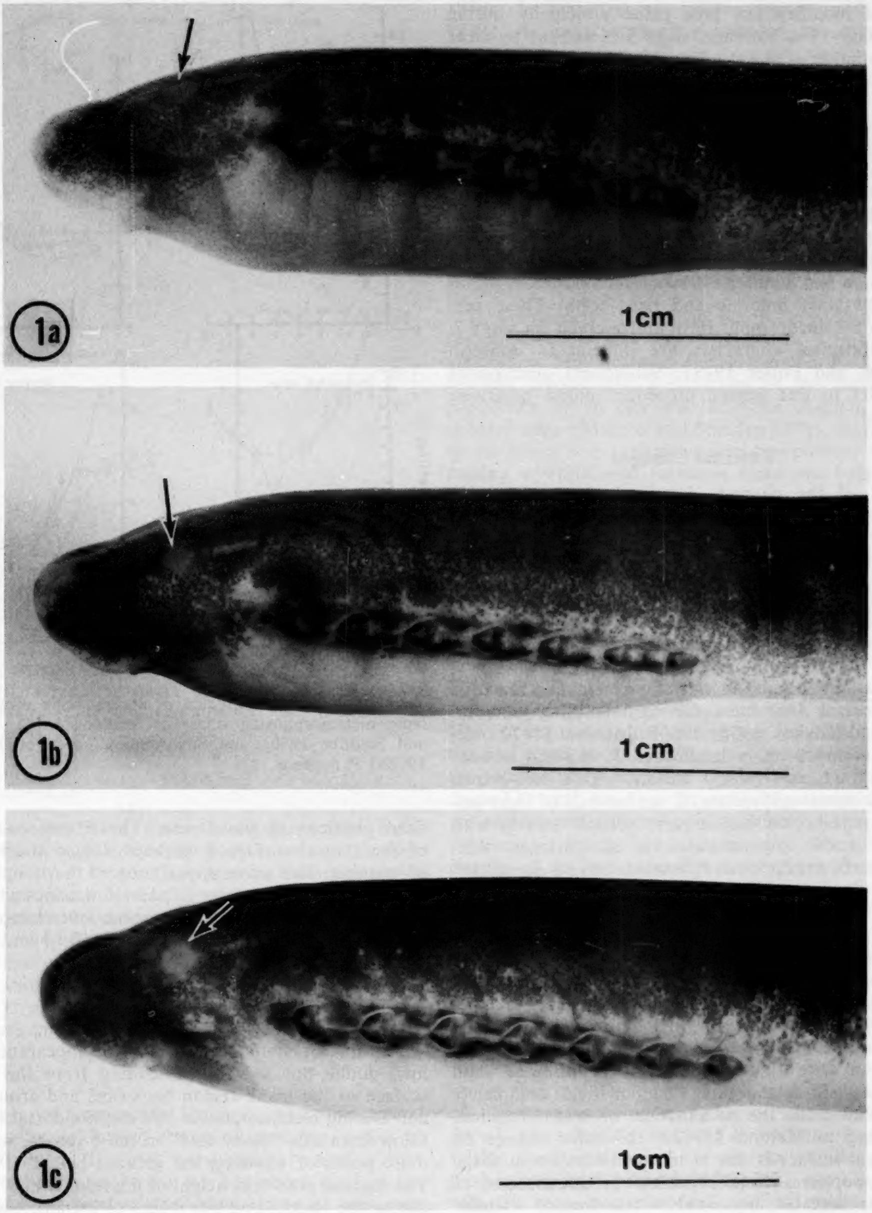


FIG. 1. Lateral view of the branchial and prebranchial regions of an ammocoete (a) and stages 1(b) and 2(c) of metamorphosis. The varying degree of development of the eye (arrow) can be seen.

external modifications take place principally during these stages. For example, stage 3 is marked by clear differentiation of the eye into a dark inner pupil and a lighter outer iris, stage 4 animals possess a continuous even ring of tissue surrounding the presumptive oral disc, and stage 5 individuals contain precursors of teeth and rudimentary fimbriae on the oral disc with the tongue-like piston making its first appearance. In stage 6 the animal develops a ventral silvery sheen, the teeth appear as short, unpigmented projections of a bicuspid or unicuspid form, and the infraoral lamina appears. This stage is clearly different from the stage 4 of Manion and Stauffer (1970), which possesses prominent marginal fimbriae and hard teeth. These features in the anadromous form are reserved for stage 7, whose terminal characters are difficult to establish (Youson and Potter 1979). Subsequent descriptions will refer to this staging procedure unless otherwise specified.

External Changes

Most of the changes described here presumably apply to all lamprey species and are a direct result of internal modifications, some of which will be referred to in greater detail in a later section.

Body Coloration

The dorsal surface of most species of ammocoetes is dark brown with the ventral surface light brown. The distribution and amount of pigmentation are used as important characters for distinguishing different species (Vladykov 1950, 1960). Manion (1972) describes ammocoetes in landlocked *P. marinus* as consisting of a typical "black" variety, with a dark-brown to black dorsal surface and a ventral half of light yellow to pale brown, and a rare "yellow" variety with modest visible pigmentation on all surfaces. Ammocoetes of anadromous *P. marinus* have a dorsal surface similar to that of "black" lampreys except ventrally they are greyish-brown (Youson and Potter 1979).

The pigmentation of both surfaces is due to the presence of melanophores in the dermis. During metamorphosis of *P. marinus* the dorsal half of the transforming individuals progressively darkens to a blue-black while the ventral half (including the area between branchiopores) attains a silvery sheen. This begins at the same time that the teeth, oral fimbriae, and piston start to appear (stage 5) but is not completely manifested until the termination of transformation. According to Manion (1972), the color change on the dorsal surface is due to the modifications in shape of melanophores from reticulate in ammocoetes to stellate–reticulate in newly transformed adults. Melanosomes (melanin-containing granules) are also more abundant and more "intensely" dispersed in the adult melanophores. Johnels (1950) also reports on the migration of pigment cells towards more superficial positions in the dermis. The silvery coloration of the ventral surface is perhaps due to the buildup of quanine. The silver appearance of the nonparasitic European brook lamprey, *L. planeri*, declines while the parasitic and anadromous European river lamprey, *L. fluviatilis*, increases its silvery sheen (Bird and Potter 1979a).

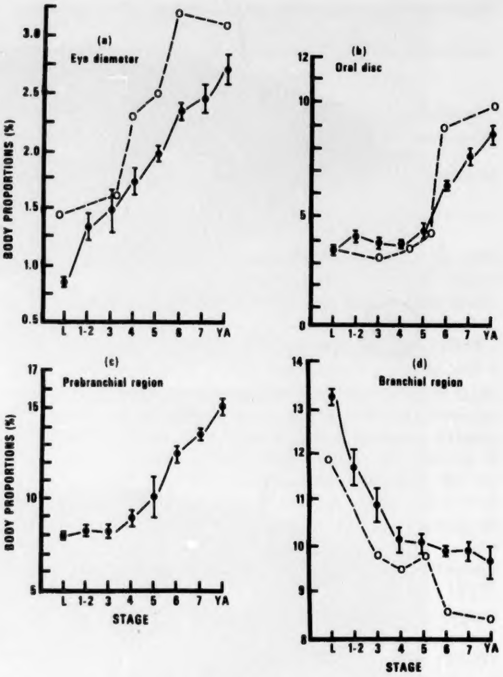


FIG. 2. Comparison of data of several body proportions from metamorphosing stages of landlocked (○, Manion and Stauffer 1970) and anadromous (●, Potter et al. 1978b) *P. marinus*.

Dorsal Fins

The fins of ammocoetes have the appearance of a low, double-notched fold extending from the dorsal surface of the trunk region backward and around the tail. During metamorphosis, two distinct dorsal fins develop from this "fleshy fold" in most genera, with the more posterior attaining the greatest height (Fig. 3). The marked growth in height of the folds, which occurs during the middle and late stages of metamorphosis in *P. marinus* (Fig. 3), can be related to the assumption of a more active mode of life by the adults. Paralleling the development of the two dorsal fins is the enlargement of the dorsal and ventral parts of the caudal fin.

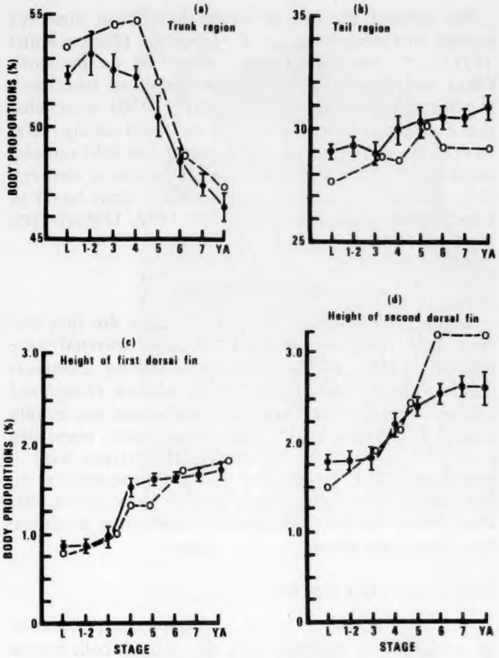


FIG. 3. Comparison of data of several body proportions from metamorphosing stages of landlocked (○, Manion and Stauffer 1970) and anadromous (●, Potter et al. 1978b) *P. marinus*.

BRANCHIOPORES

Ammocoetes have seven triangular-shaped branchiopores on each side of the body, connected in their midregion by a longitudinal furrow. Coincident with the change from a unidirectional flow of water through the gills in ammocoetes to tidal ventilation in the adult (Balabai 1946; Randall 1972; Lewis and Potter 1976), branchiopores transform to an oval shape. This modification begins relatively early in *P. marinus* (stage 3) and is ultimately accompanied by a loss of the connecting groove.

EYE

The eyes of ammocoetes are small, dark, dorsolateral patches directly behind the most posterior aspect of the oral hood. The eye is rudimentary and is subcutaneous. Changes in the eye have been used as key characters for most of the initial stages of metamorphosis (Siebold 1863; Johnels 1948; Manion and Stauffer 1970; Poltorykhina 1971), but they are particularly useful structures for denoting the very onset of the process (Youson et al. 1977; Bird and Potter 1979a, b; Potter et al. 1978b; Youson and Potter 1979). As metamorphosis is initiated, the eyes come closer to the surface and consequently appear larger. Furthermore, they are of irregular shape and of greyish coloration. Subsequent development of the eye in *P. marinus* involves initially a rounding and darkening and then the gradual differentiation into a small grey iris and large pupil. The iris gradually lightens to form a white ring surrounding a small pupil and the whole eye enlarges continually throughout metamorphosis (Fig. 2) and eventually projects laterally.

NASOPORE AND LATERAL LINE SYSTEM

In ammocoetes the single nasopore is located on the middorsal surface and is flanked by a thin, flared membrane. Modifications during metamorphosis in *P. marinus* involve first a reduction of the flaring and production of an elevated, tube-like channel with a serrated edge (Manion and Stauffer 1970). Raised pits of the lateral line system become conspicuous as lines passing upwards and forwards from just behind the oral disc to a point midway between the top of the snout and the eye.

ORAL APPARATUS

The oral hood undergoes the most dramatic and most numerous external changes, and, therefore, it received the most attention in the early literature (Müller 1856; Bujor 1891a, b). Damas (1935) and Bird and Potter (1979a) describe in detail the differences in this region in larval, transforming, and adult *Lampetra* sp. New structures formed during the transformation of the oral hood to an oral disc are oral fimbriae, teeth, the tongue-like piston, and the infraoral lamina. The dome-like oral hood of the ammocoete consists of a crescent-shaped anterior portion which ends freely as continuous anterior and lateral lips. The posterior margin of the buccal cavity is a separate, transverse lip. A network of branched oral cirri extend across the oral aperture at the posterior end of the oral cavity while smaller dorsolateral papillae are present more anteriorly. Transformation of this region begins with a thickening of the edges of the lateral and transverse lips. Microscopically, this is a thickening of the epithelium and is followed by an elevation, clumping, and branching of the anterior dorsolateral papillae.

Fusion of the posterior transverse lip with the lateral lips at their point of junction results in the formation of a continuous unindented ring of tissue around the dorsal disc relatively early in *P. marinus* (stage 4). Within the buccal funnel the anterior papillae branch further but later become reduced in number, along with the more posterior oral cirri, to reveal a small tongue-like piston just extending into the narrowed oral aperture. Small fimbriae on the edge of the oral disc, tooth precursors, and a prominent piston appear simultaneously following the loss of cirri and papillae. With the enlargement and elongation of the disc and the lengthening of the fimbriae, the animal is able to adhere to surfaces. At the same time (stage 6) the infraoral lamina appears and the teeth are conspicuous as white, blunt cusps with a unicuspid or bicuspid nature.

Subsequent development of this region during metamorphosis involves a yellowing and sharpening of both the teeth and the projections on the transverse and longitudinal lingual laminae and on the infraoral lamina. The young parasitic adults possess pigmented fimbriae and the teeth are more widely spaced and more intensely yellowed. Furthermore, infraoral lamina and lingual laminae contain more well-defined, sharper projections. It is clear that the above changes are in conformity with parasitic activity of the adult. However, as demonstrated by Bird and Potter (1979a) in *L. fluviatilis* and *L. planeri*, these changes are similar in closely related (paired) species of lamprey. This, they contend, is evidence that nonparasitic lampreys evolved from parasitic species.

BODY PROPORTIONS

Quantitative assessment of changes in body proportions has revealed a consistent pattern during the transformation of most species of lampreys (Lohnisky 1967; Manion and Stauffer 1970; Poltorykhina 1971; Potter et al. 1978b; Bird and Potter 1979b). Data from landlocked (Manion and Stauffer 1970) and anadromous *P. marinus* (Potter et al. 1978b) illustrate these consistencies (Fig. 2 and 3). Because of the variations in length of metamorphosing lampreys these data are expressed as a percentage of the total body length. The length of the oral hood of large ammocoetes is 3.5–4.0% of the total body length but, by the time feeding begins, the newly formed oral disc is about 9%. The width of the snout also increases in diameter (Manion and Stauffer 1970). In *L. fluviatilis* and *L. planeri* the disc is only 5% of the total length (Bird and Potter 1979b) and probably reflects the efficiency of the oral disc of *P. marinus* as a suction device. The timing of the increase in length of the disc is also reflected in the length of the prebranchial region which rises from 6% in large ammocoetes to 15% in young feeding adults. Internal modifications to the branchial (pharyngeal) basket (Damas 1935; Balabai 1946) which accompany the development of tidal ventilation in the adult probably accounts for a decrease in length of the branchial region but also for an initial increase in its depth (Manion and Stauffer 1970). The trunk region (from the last branchiopore to in front of the anus) makes up about 52% of the body length in an ammocoete but this drops to 46–47% in young adults whereas the tail region is ~2% longer. That the eye shows a visible increase in diameter throughout metamorphosis has been demonstrated quantitatively in *P. marinus* and in all other species of lamprey (Poltorykhina 1971; Bird and Potter 1979b). The height of the two dorsal fins increases marginally in early stages but later increases abruptly.

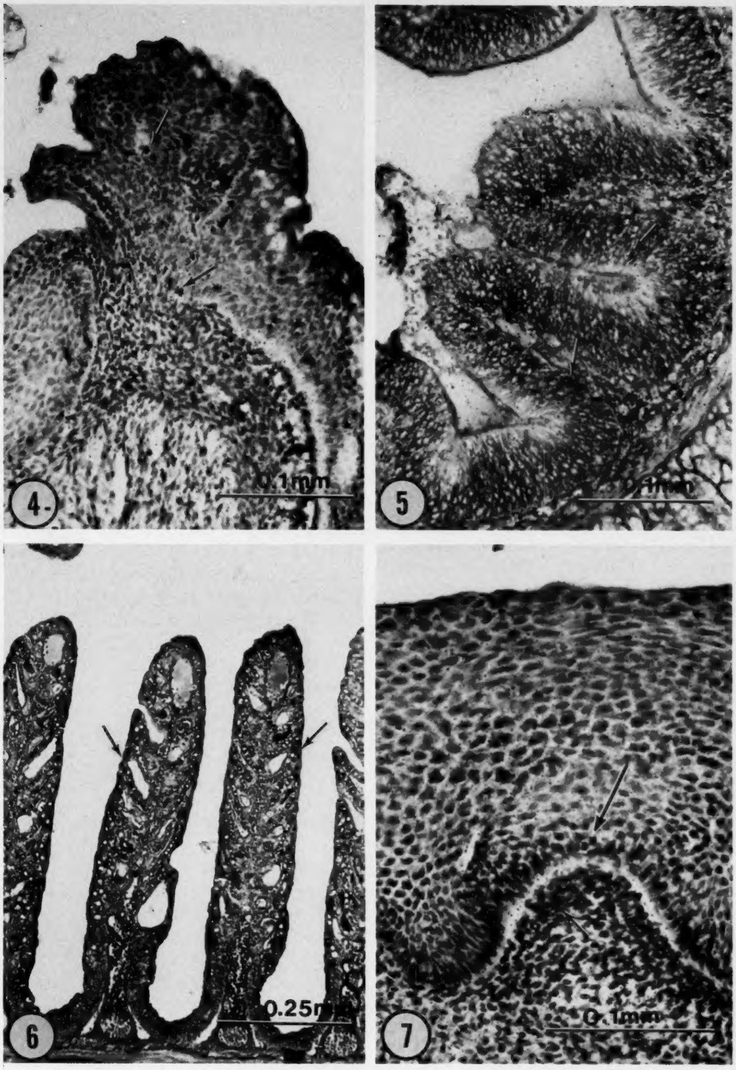
No marked changes in length have been observed during metamorphosis of *L. japonica* (Poltorykhina 1971), *M. mordax* (Potter 1970), or *L. fluviatilis* (Bird and Potter 1979b). On the basis of laboratory experiments, Manion and Stauffer (1970) concluded that *P. marinus* increased slightly in length during metamorphosis, and other data collected from field samples certainly supports the view that sea lampreys undergo little change in length in the transition from larval to young adult (Beamish and Potter 1972; O'Boyle and Beamish 1977; Potter et al. 1978b).

Internal Changes

Bujor (1890, 1891a, b, c, d, e) gave the first and only comprehensive account of most internal anatomical changes of the ammocoete during metamorphosis. These observations on *L. planeri* recognized that some new organs arise whereas others are simply modified (transformed). Since that time, numerous authors have usually concerned themselves with a single aspect of the process or have concentrated on one part of the body. These studies have shown that every body system undergoes at least some modification during this phase.

INTEGUMENTARY SYSTEM

The integument, as in other vertebrates, consists of an epidermis of epithelial cells and a thick collagenous dermis (subepidermal collagenous lamellae). Although mucous, granular, and club cells make up the epidermis in both ammocoetes and adults (Downing and Novales 1971a, b, c), the epidermis and dermal collagenous lamellae thicken during metamorphosis (Lethbridge and Potter 1980). The number of mucous cells increases dramatically in stages 1 and 2 of *L. fluviatilis* and *L. planeri* while granular cells increase steadily over the metamorphic period. There is no significant change in the numbers of club cells (Lethbridge and Potter 1980). Extensive DNA synthesis occurs in cells at the base of the epithelium in the head region of *P. marinus* throughout metamorphosis (J. H. Youson unpublished observations). This probably reflects the increase in number of cells necessary to accommodate the growth of skin over the elongating and broadening oral disc. The proliferation of the epidermis and dermis is particularly marked in the developing and elongating oral fimbriae (Fig. 4). Dermal papillae become obliterated and pits of the lateral line system become larger. The sensory, ciliated cells elongate and become arranged differently to those in the ammocoete (Bujor 1890, 1891a, e). Johnels (1950) described the dermal connective tissue of the head, anterior to the branchial region, as initially separating into layers and later reforming into a single or trilayered aponeurosis. This is accounted for by the rostrad elongation of the developing disc, the growth of the eye, and by the fact that the original dermal tissue may be too resistant to allow change.



FIGURES 4–7

FIG. 4. An autoradiograph demonstrating [^{3}H]thymidine incorporation (DNA synthesis) into cells (arrow) at the lateral margins of the oral hood of a stage 4 metamorphosing animal. This depicts the early development and elongation of an oral fimbria. FIG. 5. An autoradiograph revealing DNA synthesis in cells (arrows) of the developing nasal sac in a stage 2 animal. FIG. 6. Adjacent gill lamellae from a transforming landlocked *P. marinus* (stage 5) appear to be fused to one another (arrows). FIG. 7. An autoradiograph of a stage 4 animal showing early tooth development as indicated by DNA synthesis in cells at the base of the thickened oral epithelium (large arrow) and in the supporting connective tissue core (small arrow).

SKELETAL SYSTEM

The notochord is the major supportive structure in the trunk and tail regions of lampreys. The cartilaginous cranium and the visceral skeleton provide an additional supporting skeleton to the head and branchial region, respectively. The cylindrical notochord of ammocoetes extends from near the eyes to the posterior tip of the body and is tapered at both ends. It is composed of an inner core of vacuolated cells and an outer multilayered sheath of fibrous and cellular elements. Bujor (1890) reports that the anterior end of the cord elongates during metamorphosis, although no mention is made of this by those other investigators who have studied the head in detail (Kaensche 1890; Damas 1935; Johnels 1948). Bujor (1890, 1891a, e) also indicated that the fibrous elements of the sheath become more compact and therefore more like hyaline cartilage. Neurapophyses (arcualia) arise from embryonic connective tissue present in the ammocoete and eventually become cartilaginous (Bujor 1890).

Probably the most extensively studied feature of internal transformation is the modification to the cranium (Parker 1883; Bujor 1891a, b, e; Damas 1935, 1942; Johnels 1948). Many studies were inspired by the desire to show the relationship between mucocartilage, hyaline cartilage, and fibrous connective tissue of the ammocoete cranium with the cartilaginous cranium in the adult. It is beyond the scope of this review to describe in detail the various morphogenetic events which lead to this transformation. Suffice it to say that the ammocoete is the only vertebrate which utilizes mucocartilage as a large part of its endoskeleton and this is confined mainly to rostral parts of the cranium. Mucocartilage disappears or transforms into adult hyaline cartilage during metamorphosis. For example, the cartilage of the tongue-like piston originates in the ventromedial, longitudinal bar of ammocoetes. This bar projects into the floor of the buccal funnel and is made up of mucocartilage. In contrast, the ammocoete velar skeleton disappears. The events of the process, the importance of the changes to the adult, and the phylogenetic significance are summarized and well illustrated by Johnels (1948).

The homology of the visceral skeleton of lampreys to that of gnathastome fishes has long been debated (Johnels 1948). Unlike the cranium, the branchial basket is made up entirely of hyaline cartilage in the ammocoete. During metamorphosis blastematic primordia on each arch develop into cartilaginous bars whereas cartilaginous rings around the gill slits form directly from mesenchyme.

There is a paucity of information on changes occurring in the supporting skeleton of the fins. However, there does seem to be an increase in width and length of the cartilaginous fin rays (Rovainen and Birnberger 1971).

MUSCULATURE

Kaensche (1890) first reported that changes occur in the musculature of lampreys during metamorphosis. As might be expected, he was mainly concerned with the visceral and parietal muscles in the head and therefore little information is provided on trunk muscles. The most recent survey of the musculature of lampreys is provided by Marinelli and Strenger (1954).

As in other vertebrates, the trunk masculature of adult lampreys is in the form of segmentally arranged myotomes but the arrangement of the muscle fibers within these myotomes is unique to vertebrates and also differs from that of the ammocoete (Nakao 1977). The observations of Peters and MacKay (1961) and of Teräväinen (1971) indicate that this difference is a result of a progressive change rather than one which occurs at metamorphosis. According to Bujor (1891a, b, c) the trunk muscles over the branchial basket stretch out more than in the ammocoete. The increase in dimension of the dorsal fin during metamorphosis is partially due to an increase in volume of the muscle from strands of narrow fibers in ammocoetes to several layers of fiber bundles in the adult (Rovainen and Birnberger 1971).

Damas (1935) performed an extensive examination of peripheral (parietal) and visceral muscle of the head of transforming lampreys. Ammocoete visceral muscle is almost completely destroyed with only two little muscle bundles of the velum persisting. The process of degeneration involves an initial proliferation of connective tissue between the muscle fibers resulting in their separation and a subsequent vascular invasion of engorged blood vessels. This is followed by granulation of the muscle fibers, death of the cells, and phagocytic activity by leucocytes. Degeneration does not occur in all muscle cells at the same time and the process occurs most rapidly in the velum. All the stages of degeneration can be observed at one time in the anterior portion of the lip, as the fibers on the outside of the muscles are destroyed first and those in the center gradually succumb.

Development of adult muscle accompanies degeneration of larval muscle. The first to form appears between the larval muscle and oral mucosa and others between the elastic skeleton of the ventral crest and the mucosa. The cells do not dedifferentiate from cartilage cells (Kaensche 1890; Bujor 1891a, b) but originate in mesenchyme. The muscles develop in very close relationship to the transforming cartilage upon which they eventually insert. The muscles related to the developing piston appear to arise in mesenchyme close to the degenerating endostyle. The functional morphology of the various visceral muscles formed during metamorphosis is described by Damas (1935).

The parietal muscles consist of the dorsal epitrematic (epaxial) myomeres and the more ventral hypotrematic (hypaxial) muscles. In the head, not much change occurs in the epitrematics but during the development of the eye, the lateral epitrematic myomeres are divided in half. The most superior portion becomes the corneal muscle while the rest becomes deeply embedded and attaches to sheaths of the visceral muscle. The hypotrematic muscles become greatly enlarged because of the elongating head. Furthermore, a subocular muscle develops from a mass of undifferentiated cells present in the ammocoete. At the beginning of metamorphosis, this mass is replaced by a cord which first elongates and then forms into muscle. Damas (1935) believes that the mass forms at the time of development of myomeres but does not differentiate until metamorphosis. More posteriorly the parietal muscle undergoes little change.

BRAIN AND SPINAL CORD

Schober (1964) and Healey (1972) have provided the most recent accounts of the structure of the central nervous system in lampreys. In summary, the most anterior prosencephalon consists of a telencephalon, with olfactory bulb and cerebral hemisphere portions, and a diencephalon with poorly developed thalamic, hypothalamic, and hypophyseal regions, but with a prominent pineal and parapineal on the roof. The mesencephalon is characterized by the paired optic lobes in the posterior region of the tectum. The posterior rhombencephalon is composed of the metencephalon, with its small cerebellum, and the myelencephalon consisting of the medulla oblongata. The spinal cord extends posteriorly from the medulla oblongata throughout the length of the animal.

Changes that occur in the central nervous system during metamorphosis have mainly been documented through comparative observations of ammocoetes and adults (Healey 1972) rather than from direct observations on transforming individuals. Bujor (1891c), however, noted changes occurring in the spinal cord, forebrain, optic tectum, and the infundibulum. Although the cells of the spinal cord become elongated, they retain similar or identical functions (Rovainen 1978). The increase in volume of the forebrain (telencephalon portion) is caused by the enlargement of the ganglia (Bujor 1891c) by growth of the existing neurons and not by increase in numbers of neurons (Rovainen 1978). Bujor (1891c) also felt that during the early stages of metamorphosis, the optic tectum is invaded, particularly the grey matter, by large numbers of undifferentiated cells, but ultimately these transform into nerve cells. The apparent enlargement of this region in adults by four times the size seen in ammocoetes (Kennedy and Rubinson 1977) may be the result of mitosis (Pfister 1971) which ceases in medium-sized ammocoetes well before metamorphosis.

The infundibular lobe of the mesencephalon takes on a bilobed external appearance. The dorsal thalamus is three times its size in ammocoetes. Its lateral region has more cells perhaps from lateral migration of cells from the thinner periventricular region (Kennedy and Rubinson 1977). Ipsilateral retinothalamic projections to the pretectum and optic tectum develop during metamorphosis (Kennedy and Rubinson 1977). Differences also exist between the neurons in the optic tectum of early and late transformers at which time immature nerve cells differentiate (Kennedy and Rubinson 1978). Although Damas (1935) refers to the presence of cranial ganglia during metamorphosis, there are no other reports of changes in either cranial or spinal nerves during this phase of the life cycle. In fact, Homma (1978) has recently shown the motoneurons of the trigeminal motor nucleus in the floor of the fourth ventricle to remain in a similar position despite the fact that they innervate dissimilar muscles of the oral cavity in adults and larvae. Although the neurons are structurally similar, there is no evidence that they are the same or different cells.

PINEAL (EPIPHYSEAL) COMPLEX

A review of the morphology of this structure has recently been provided (Eddy 1972). Lying above the diencephalon and just beneath the integument are a pineal and a parapineal which do not differ in adults and larvae of *Lampetra* and *Petromyzon* species (Studnicka 1893, 1899, 1905; Eddy 1970). However, the southern hemisphere genera, *Geotria* and *Mordacia*, differ in that *Mordacia* has no parapineal and during metamorphosis the parapineal of *Geotria* grows to the same size as the pineal and takes up a different position from that of the ammocoete (Eddy and Strahan 1970). The pineal grows subsequently to become larger than the parapineal.

Preliminary observations on larval, metamorphosing, and adult anadromous *P. marinus* have revealed an identical pattern to that described for *Geotria* (W. C. Cole and J. H. Youson unpublished data). Cytological changes accompanying metamorphosis in *Mordacia* involve a reduction in thickness of subepidermal connective tissue, an increase in the relative size of the lumen, and a decrease in size of the retina (Eddy and Strahan 1970). The proximal portion of the pineal stock becomes lightly displaced to the left resulting from further development of the right habenular ganglion. The possible significance of these structures to metamorphosis will be discussed later.

HYPOPHYSIS

The lamprey pituitary consists of a simple neurohypophysis and an adenohypophysis divided into three regions: pro-, meso-, and meta-adenohypophyses (Larsen and Rothwell 1972). During development these latter three regions originate from ectoderm extending down as a nasohypophysial (nasopharyngeal) stalk (Leach 1951). No connection exists between the stalk and the adenohypophysis in ammocoetes. Prior to the first signs of external metamorphosis a connection between all three regions of the adenohypophysis and the stalk is reestablished as the stalk extends posteriorly (Leach 1951; Thompson 1971). This connection is subsequently lost during later stages of metamorphosis but the adenohypophysis, particularly the meta-adenohypophysis, becomes more compressed against the neurohypophysis as the nasopharyngeal canal develops below (Van de Kamer and Schreurs 1959).

The variety of cell types present in the lamprey adenohypophysis has been reviewed by Larsen and Rothwell (1972) and Percy et al. (1975). In the ammocoete, the pro-adenohypophysis contains numerous granulated (basophilic, chromophilic) cells whereas nongranulated (chromophobe) cells are more characteristic of the meso- and meta-adenohypophyses. In general, metamorphosis in landlocked *P. marinus* seems to result in more granulated (chromophilic) cells in all regions, perhaps through differentiation from chromophobes (Percy et al. 1975). Since the function of the cell types has never been definitely established, the significance of this transformation is not known. Van de Kamer and Schreurs (1959) report that "thyrotrophs" in *L. planeri* become active at the very end of larval life and reach peak activity during metamorphosis.

SENSE ORGANS

The embryogenesis, morphology, and histology of the eyes of larval and adult lampreys have recently been reviewed (Kleerekoper 1972). A thorough account of metamorphic changes which occur in the entire eye is provided by Bujor (1891c). He describes the following events: (1) the shape of the eye changes from oval to nearly spherical; (2) the layers of the subdermal connective tissue and the dermis are nearly entirely resorbed; (3) a clearer distinction occurs between the sclera and choroid layers as a result of the gradual invasion of the choroid by large numbers of blood vessels and the increase in numbers of pigment cells; (4) the lens enlarges to take up nearly all the vitreal chamber; (5) the iris, the anterior continuation of the pigmented layer of the choroid, becomes very heavily pigmented. Earlier the "membrane argentee" appears as two or three layers of cells, one of fusiform cells and the other plate-like cells, which contain yellow crystals of quanine; (6) the formation of an inner layer of epithelial cells on Descemet's membrane; (7) formation of a ciliary ligament within the vitreous humor; (8) increase in amount of pigment around the circumference of the eye. Bujor (1891c) makes very little mention of changes to the retina but recently Dickson and Collard (1979) have shown in *P. marinus* ammocoetes that the retina is completely undifferentiated with the exception of a small area surrounding the optic nerve end. At the onset of metamorphosis, differentiation of the remainder takes place in a radial fashion from the optic nerve.

The structure of the lamprey ear (labyrinth and acoustic organ) and the lateral line system have been recently reviewed by Kleerekoper (1972). There appear to be no studies on the transformation of these structures during metamorphosis. According to Thornhill (1972), the labyrinth of a medium-sized ammocoete is already structurally similar to that of an adult but is of smaller size.

The nasal apparatus of larval and adult lampreys has received considerable attention and its transformation during metamorphosis has been thoroughly described (Lubosch 1905; Imamura 1928). In ammocoetes, the external nares lead into a smooth-walled nasal sac and a tapering strand of tissue, the nasopharyngeal stalk, which is connected to the ventroposterior part of the sac. By early stages of external metamorphosis, the smooth-walled nasal sac becomes highly folded because of longitudinal elevation of the epithelium and its supporting connective tissue (Leach 1951). The folds extend into the lumen of the sac and diverticulation of the epithelium results in the formation of small glands or vesicles which extend into the underlying connective tissue. In anadromous *P. marinus*, only slight folding is seen in stages 1 and 2 but in stage 3 it is extensive. Autoradiography with [^{3}H]thymidine indicates intense DNA synthesis in both the connective tissue core and the epithelium of the longitudinal folds of all early stages of metamorphosis (Fig. 5).

CIRCULATORY SYSTEM AND BLOOD MORPHOLOGY

It is evident from the most recent review of lamprey circulation (Fänge 1972) that there is little information on changes in circulation that occur at metamorphosis. Fänge (1972) does mention that the left ducti Cuvieri of the ammocoete disappears (Hatta 1923) and that sinuses, not typical of ammocoetes, develop throughout the body during metamorphosis. Maskell (1931) and Minelli and Rossini (1961) also report that the original hepatic portal vein of ammocoetes diminishes in size and a new portal vein is formed.

Other reports deal specifically with changes in circulatory patterns within organs, for example, those occurring in the intestine (Baxter and Robinson 1942; Baxter 1957; Percy and Potter 1979). The most recent work of Percy and Potter (1979) on *L. fluviatilis*, however, is the most comprehensive account of direct observations on metamorphosing specimens. The alimentary canal shows the vascular features of the adult 6–8 wk after the start of external metamorphosis. This includes the development of a typhlosolar vein as the main venous return and vascular couples, which result in blood flowing in opposite directions in veins and arteries. The degeneration of the larval opisthonephros and its vascular supply is accompanied by development of renal arteries (Ooi and Youson 1977) and secondary venous connections (Baxter 1957; Youson and McMillan 1971b) in the new adult opisthonephros. There are no reports on specific modifications to the heart, although the heart ratio (heart weight/body weight × 100) increases dramatically during metamorphosis (Claridge and Potter 1974). This change is almost certainly related to a higher rate of oxygen consumption in the adult (Fänge 1972; Claridge and Potter 1974).

The intestinal typhlosole and the anterior nephric fold are the principal sites of haemopoiesis in ammocoetes (Jordan and Speidel 1930), but as these structures involute during metamorphosis their function is taken over by the fat column lying above the nerve cord (George and Beamish 1974; Percy and Potter 1976, 1977; Potter et al. 1978a). The transference of haemopoietic cells from these sites to the fat column is a gradual process beginning at the first signs of external metamorphosis in *L. fluviatilis* and *L. planeri* (Percy and Potter 1977). Although it seems that blood cell formation starts to decline just before the onset of external metamorphosis in *Lampetra* spp. (Percy and Potter 1977), DNA synthesis is still very extensive in these cells in the typhlosole (Youson and Connelly 1978) and the larval nephric fold (Ooi and Youson 1977) of *P. marinus*. There appears to be no change in cell types during metamorphosis but erythrocyte nuclei of ammocoetes occupy a much greater area of the cell than those of adults (Potter et al. 1974).

RESPIRATORY SYSTEM

The respiratory apparatus and digestive system undergo important modifications to accommodate the feeding habit of the adult. This involves development of an adult oesophagus (foregut) from the dorsal fold of the pharynx (Weissenberg 1925, 1926; Boenig 1927, 1928; Keibel 1927; Kraentzel 1933; Hardisty et al. 1970) and restructuring of the gill pouches and their supporting tissue (Balabai 1946). At the same time the posterior end of the pharynx loses its connection with the former ammocoete oesophagus. As ventilation of the gills is usually tidal in the adult (Dawson 1905; Randall 1972), these modifications, and the positions and action of the muscular velum, can prevent water flow.

The specific events of the transformation of the branchial region have not been thoroughly documented, although Balabai (1946) refers to changes in blood sinuses, the segregation of gill pouches from the branchial septa, the constriction of internal branchial clefts to small openings, and the development of medial walls. The gill lamellae, the branchial skeleton, and the musculature remain relatively unchanged (Balabai 1946). More recent microscopic studies on transforming stages of landlocked *P. marinus* (Freeman 1974) demonstrate collapsed lamellae to the extent that they appear to adhere to one another (Fig. 6). This feature, appearing at stages 5 and 6, is accompanied by degeneration of many of the cell types along each lamellae. Degeneration is also noted in anadromous *P. marinus* but there is also extensive DNA synthesis occurring among the lamellar (respiratory) epithelial cells (Peek and Youson 1979). This proliferation may be responsible for the replacement of the epithelial cells lost through degeneration and/or contribute to the lengthening of the lamellae. Lewis and Potter (1976) have found that, although the total gill areas of ammocoetes (*Lampetra* spp.) and late metamorphosing animals are not different, the total length of the filaments and the total length of the secondary lamellae is greater in these metamorphosing stages. However, the bilateral area of the lamellae is greater in ammocoetes.

DIGESTIVE SYSTEM

Modifications to the digestive system include the development of teeth, a tongue-like piston, and a new oesophagus and major restructuring of the intestine and its circulation. Significant changes also take place in the liver and the exocrine pancreatic tissue. Since teeth are a conspicuous feature of the adult, their development received considerable attention by early morphologists (Kaensche 1890; Bujor 1891a; Warren 1902; Hansen 1919). More recently, Sognaees and Lustig (1955) and Trott and Lucow (1964) have provided detailed histological and histochemical accounts of adult teeth, and Manion and Piavis (1977) reported on the development and structure of teeth during the life cycle of landlocked *P. marinus*. Observations of metamorphosing anadromous *P. marinus* have revealed that the first sign of development is a thickening of the stratified squamous epithelium and its underlying connective tissue. This results at stage 2 in the elevation of the former ammocoete dorsolateral papillae. By stage 4, the reduction of these papillae is accompanied by the extension of a dome-shaped wedge of proliferating connective tissue cells and fibers into the overlying thickened, and proliferating stratified squamous epithelium (Fig. 7). Stage 6 demonstrates the most pronounced development of teeth with animals in the group possessing the first sign of a keratinized cone overlying a stellate reticulum (Manion and Piavis 1977). The basal cells in the epithelium below the keratinous zone demonstrate active DNA synthesis. By stage 7 the teeth have three cones of keratinized material separated by reticular layers, but extensive DNA synthesis continues in the basal cells of the mucosal epithelium. While the teeth are developing, widespread tissue proliferation at the margins (lips) of the buccal cavity results in the development of fimbriae. The proliferation of tissue is evident in stage 4 but small mucosal projections do not appear until stage 5 (Fig. 4).

The tongue appears in sections in animals of stage 3 but does not contain a supporting core of cartilage until stage 5 at which time it extends well forward into the posterior portion of the buccal cavity. At the same time the surrounding mucosal epithelium is thickened and several cone-shaped papillae (teeth precursors) are formed. Subsequent development involves the keratinization of the papillae to form the transverse and longitudinal lingual laminae, and the maturation of the supporting cartilage. The tooth-like processes of the infraoral lamina also result from the keratinization of the mucosal epithelium, but this does not appear until stage 7.

The adult oesophagus (foregut) begins as a solid cord of cells originating from a dorsal fold of the pharynx (Weissenberg 1925, 1926; Boenig 1928; Keibel 1927; Kraentzel 1933). A lumen forms in this cord by the gradual fusion of vacuoles throughout the length of the cord in parasitic species, but the lumen is never completely patent in nonparasitic species (Hardisty et al. 1970). The resulting new oesophagus is originally closed at its point of junction with the anterior intestine (midgut). It is clear from observations on *Lampetra* spp. that development of the oesophagus is a prolonged process which may not be complete for up to 4 mo after the start of metamorphosis (Hardisty et al. 1970). During this time the typhlosole and the coelic artery migrate from left to right over the dorsal surface of the gut. Furthermore, the typhlosole contains the caudal part of the pancreas, the junction of the oesophagus and anterior intestine is at the anterior end of the liver (posterior end in ammocoete), and the junctional diverticulum is enlarged and surrounds the cranial portion of the pancreas (Boenig 1928; Hardisty et al. 1970). In *P. marinus* the small dorsal cord still appears attached to the pharyngeal wall in stages 1 and 2 and at stage 3 has become somewhat crescent-shaped but remains connected (Fig. 8). In stage 4 the cord is circular in transverse section and is greatly enlarged but, by stage 5, short longitudinal folds appear in a narrow lumen. The short primary and secondary folds in stage 6 have elongated immensely by stage 7.

Although the remainder of the alimentary tract of the ammocoete is retained, it becomes modified, principally through the acquisition of longitudinal folds. Transformation begins first in the anterior intestine at stage 4 in *P. marinus* (Youson and Connelly 1978) and involves proliferation of the mucosal epithelium and its supporting core of connective tissue and muscle. Primary (longest), secondary, and tertiary (shortest) folds are formed. The ciliated, columnar-absorptive, and secretory cells of the anterior intestine and the absorptive cells of the posterior intestine of ammocoetes (Hansen and Youson 1978) are primarily replaced by aborptive, secretory, and a few ciliated cells (Yamamoto 1965) in the adult. This process in stage 4 of *P. marinus* is marked by the appearance of large lateral intercellular spaces in the epithelium, autolysis of cells (Fig. 9) and their subsequent removal into the intestinal lumen, and proliferation and differentiation (perhaps redifferentiation) of the epithelium. Degeneration of secretory cells at earlier stages suggest that the adult secretory cells differentiate during metamorphosis and are therefore not the same cells as in ammocoetes.

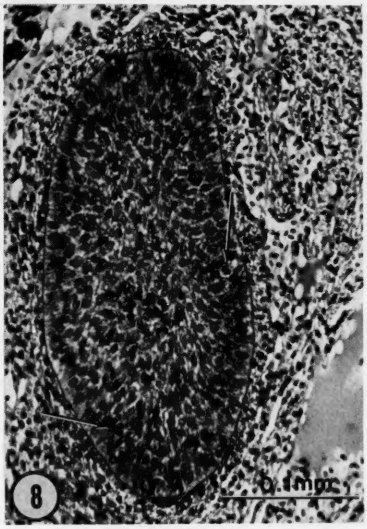
The modifications to the liver principally involve the biliary tree (Maskell 1932). The bile canaliculi (tubular lumina), bile ducts, and the intrahepatic gall bladder of the ammocoete completely disappear at metamorphosis in *P. marinus* and are not replaced (Youson and Sidon 1978). This process begins at the onset of metamorphosis and involves autolysis of the ductular epithelium and the replacement of these areas by connective tissue and, eventually, by the liver parenchyma cells. The events are most dramatic by stages 3 and 4, and only a few ducts persist in stages 5 and 6. All apparent exocrine function is lost by stage 7. A progressive accumulation of bilirubin is seen in the hepatocytes from stage 4 onwards. Maskell (1932) also reports on the lengthening of the liver and changes in its shape during metamorphosis of *Geotria*.

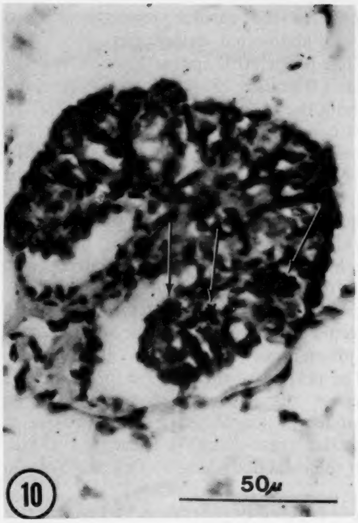
In larval lampreys of the northern hemisphere there is no discrete exocrine pancreas but instead secretory cells are dispersed in the mucosa of the anterior intestine (Barrington 1972). In *Geotria*, a completely separate collection of secretory cells is present in the wall of an intestinal diverticulum (Maskell 1931). During metamorphosis of *Lampetra* spp. (Barrington 1945) and *Petromyzon*, a blind diverticulum develops at the oesophageal–intestinal junction (Boenig 1928) and it contains numerous secretory cells. These cells are also formed throughout the intestinal epithelium and have properties suggestive of pancreatic exocrine cells (Barrington 1972). The diverticulum of the *Geotria* ammocoetes disappears at metamorphosis (Maskell 1932).

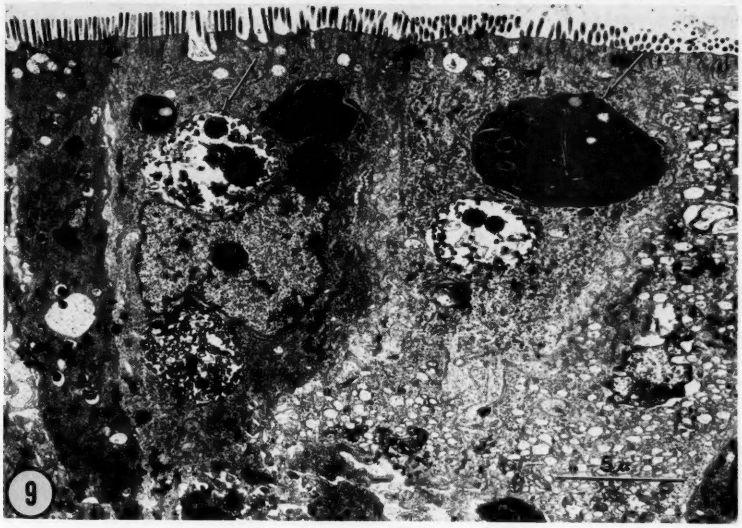
REPRODUCTIVE SYSTEM

Earlier reports deal with aspects of gonadal structure and development in metamorphosing *Lampetra* spp. (Wheeler 1899; Weissenberg 1925; Hardisty et al. 1970; Hardisty 1971). Specific differences are noted between the parasitic *L. fluviatilis* and the nonparasitic *L. planeri* in that the former shows no rapid growth and no atresia of oocytes during metamorphosis. Follicular atresia (Busson-Mabillot 1967) and growth of the oocytes (Weissenberg 1925; Hardisty et al. 1970; Hardisty 1971) in *L. planeri* have been thoroughly documented. At metamorphosis the spermatogonia of *Lampetra* spp. undergo mitotic division in the testis. This results in an increase in number and size of lobules and is particularly evident in *L. planeri* (Hardisty et al. 1970). By the end of external metamorphic change, *L. planeri* have a greatly enlarged testis which contains cells in meiotic prophase.

Lewis and McMillan (1965) provide the only insight into gonadal changes occurring during metamorphosis of *P. marinus*, and these changes are inferred from observations on ovaries of large ammocoetes and of adults. During metamorphosis there is little development of oocytes over the condition in large ammocoetes but there is an increase in vascularization, in the amount of stromal tissue, and in the number of follicular cells surrounding each oocyte. These increases are no doubt caused by proliferation of tissue similar to that observed in *L. planeri* (Hardisty et al. 1970). In the testes and ovaries of metamorphosing anadromous *P. marinus* many cells undergo DNA synthesis. Particularly evident in stage 4, the proliferating cells in the ovary are located at the periphery of the oocytes and are probably granulosa (follicular) cells, while the smaller testes show larger numbers of proliferating cells in both the stroma and germinal cysts (Fig. 10).







FIGURES 8–10

FIG. 8. The dorsal cord of epithelial cells in a stage 3 animal is the forerunner of the adult foregut (oesophagus). Note numerous mitotic figures (arrows). FIG. 9. An electron micrograph of the intestinal epithelium of a stage 2 animal shows that numerous cytoplasmic vacuoles containing a variety of cell debris (arrows) are already present in the cells. FIG. 10. An autoradiograph revealing DNA synthesis (arrows) in cells of the testes from a stage 1 animal.

URINARY SYSTEM

Changes occurring in the urinary system at metamorphosis were recognized by early microscopists in *Lampetra* spp. (Schneider 1874; Vialleton 1890; Wheeler 1899). Observations have since been made on landlocked *P. marinus* (Youson 1970) and on the anadromous form (Ooi 1977). Ammocoetes possess paired pronephroi in the cardiac region and opisthonephroi in the abdominal cavity throughout this lengthy phase. The pronephroi appear at an early stage of development (Wheeler 1899; Hatta 1900) and atrophy throughout the remainder of larval life (Bowen 1969). There are no descriptions of the fate of this structure during metamorphosis, but the pericardial cavity contains only a small portion of the pronephros in the adult.

The nephrons of the ammocoete opisthonephroi are located within the anterior portion of paired longitudinal nephric folds which project ventrally into the body cavity from either side of the middorsal line. The posterior portion of each nephric fold contains a cord of nephrogenic tissue from which the adult kidneys (definitive opisthonephroi) arise (Ooi and Youson 1976, 1977). The portion of the nephric fold taken up by the ammocoete kidney increases dramatically in the first years of larval life, so that in ammocoetes of metamorphosing size (year-class V+), each larval kidney is ~17% of the total body length (Ooi and Youson 1977).

Although there is some degeneration of the anterior tip of the nephric fold during the larval phase (Wheeler 1899), metamorphosis is marked by a complete regression of the larval opisthonephroi in the anterior portion of this fold (Youson 1970; Ooi and Youson 1979). Degeneration occurs first at the anterior tip of the larval opisthonephros and gradually extends posteriorly. Although subtle changes are evident in this region even at stage 1, autolysis is clearly evident in the tubules and renal corpuscles of animals of stages 3 and 4. Phagocytic activity by macrophages is particularly evident in the renal corpuscle (Ooi and Youson 1979).

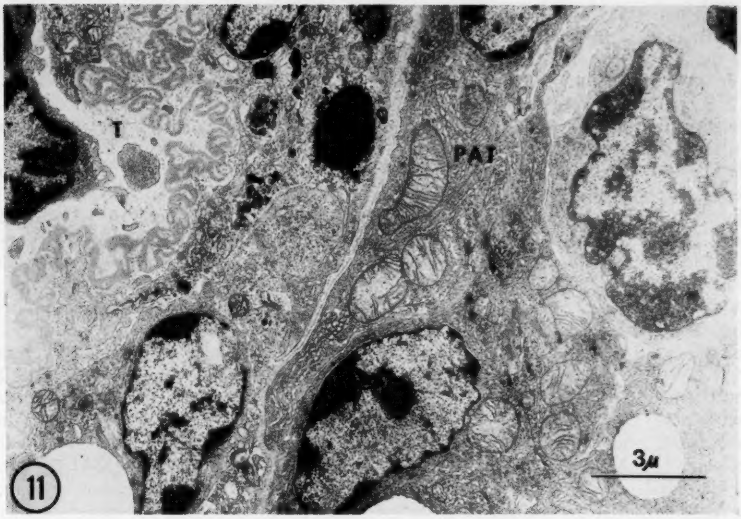
Degeneration is accompanied by development of the definitive adult opisthonephroi along the remainder of the nephric fold extending to the cloaca. The new nephrons appear synchronously along the entire length of the nephrogenic cord posterior to the ammocoete kidney (Ooi and Youson 1977). The larval kidney does not contribute to this new adult structure. The renal corpuscle (Youson and Ooi 1979) and the epithelium of the tubules (Ooi 1977) seem relatively well differentiated by late stage 4. The early stages of metamorphosis involve proliferation and growth of the renal corpuscle and more proximal segments of the tubules, but by stage 5, DNA synthesis is most evident in the ventral part of the fold (Ooi and Youson 1977) where the typical parallel system of tubules develop (Youson and McMillan 1970, 1971a). The early and rapid development of the definitive kidney is obviously related to the degeneration of the larval kidney and the immediate need for an organ for both osmoregulation and for excretion of nitrogenous waste.

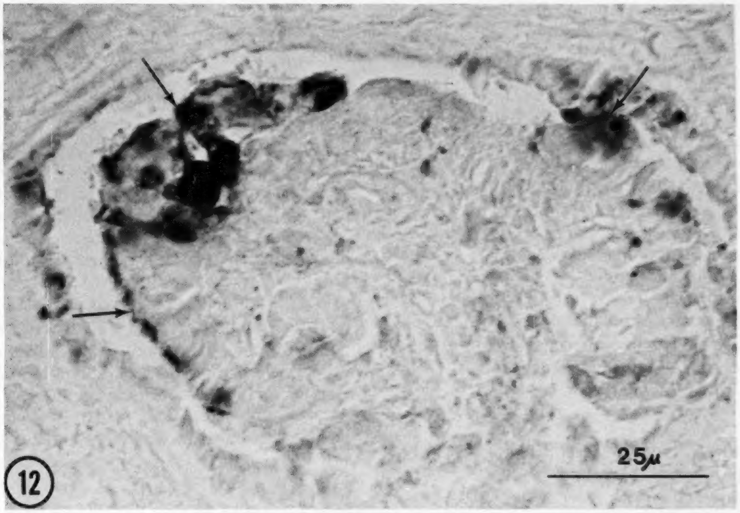
ENDOCRINE SYSTEM

Ammocoetes possess several other tissues besides the pineal and hypophysis which secrete hormones directly into the blood stream. The interstitial tissues of the testes and ovary are not developed and there appears to be no difference in structure or distribution of catecholamine-containing cells in larvae and adults (Paiement and McMillan 1975). On the other hand, Sterba (1955) refers to the prominence of adrenalin-producing cells at the beginning of metamorphosis in *L. planeri*. The enterochromaffin cells of the epithelium of the alimentary canal do not seem to vary in number and appearance in larvae and adults.

The presumed homologue to the mammalian adrenal cortex is located in ammocoetes and adults within the pronephroi (Seiler et al. 1970; Hardisty and Baines 1971; Hardisty 1972a; Seiler and Seiler 1973), along those portions of the great dorsal vessels which are contained within the abdominal cavity (Seiler and Seiler 1973; Youson 1973a), and in the opisthonephroi (Youson 1972, 1973a, b). The cells of this presumed adrenocortical tissue (PAT) or interrenal tissue (Hardisty 1972a) demonstrate all ultrastructural characteristics of steroid-producing cells but histochemical procedures do not reveal Δ^5-3β hydroxysteroid dehydrogenase, an enzyme typical of most cells synthesizing steroids. Sterba (1955) suggests that the cells of presumptive adrenocortical tissue (PAT) gradually increase in number during larval life but have a rapid period of growth at the beginning of metamorphosis. He intimates that PAT may have something to do with controlling the onset of metamorphosis. There has been no detailed analysis of the fate of PAT during the metamorphic process but Hardisty (1972b) indicates large number of cells in the pronephric area of recently metamorphosed *L. fluviatilis*. Seiler and Seiler (1973) also describe in *L. planeri* an enlargement of cell cords in the pronephric region due to the addition of cells rather than by coalescence of smaller groups. Mitosis is evident at the periphery of cords of cells which become characteristically arranged in a dorsoventral direction between the great dorsal vessels and the blood sinuses. The PAT confined within the larval opisthonephros undergoes degeneration during metamorphosis of *P. marinus* (Ooi 1977; Ooi and Youson 1979). It is of interest that this process of degeneration occurs at a much later period than that taking place in the surrounding nephric tissue (Fig. 11).

That the larval endostyle (subpharyngeal gland) undergoes transformation to become a thyroid gland was recognized by early microscopists (Schneider 1879). This process has been documented in *L. fluviatilis* (Kraentzel 1933), *L. planeri* (Leach 1939), and in landlocked (Marine 1913) and anadromous (Wright and Youson 1976; Wright 1978) *P. marinus*. Marine (1913) recognized that the initiation of the transformation of the endostyle began prior to the beginning of the change in external characters and this has since been substantiated by observations on anadromous *P. marinus* (Wright and Youson 1976; Youson et al. 1977). Shrinkage of the endostyle is accompanied by degeneration and complete loss of glandular tracts





FIGURES 11–12

FIG. 11. An electron micrograph of a portion of the larval opisthonephric kidney from a stage 5 animal showing the advanced stage of degeneration of a kidney tubule (T) with adjacent presumptive adrenocortical tissue (PAT) still intact. FIG. 12. A light micrograph demonstrating the immunocytochemical localization of thyroglobulin (arrows) in the transforming endostyle of a stage 3 animal.

and their type 1 cells by stage 4. Immunocytochemistry (Fig. 12) suggests that thyroglobulin is either stored or synthesized during the transformation process (Wright 1978) and autoradiography has shown that the epithelium also retains the ability to bind iodine (Wright and Youson 1976). Thyroid follicles seem to develop from epithelia at the angles of the endostylar lumen and also from isolated cell masses. Although all cell types of the endostyle, except type 1 cells, may be involved in formation of follicles, the incorporation of iodine and the accumulation of thyroglobulin in newly formed follicles particularly reflects the involvement of types 2, 3, and 5 cells. The endostyle is almost completely replaced by thyroid follicles by stage 5 (Wright 1978).

In *Lampetra* spp. the endocrine pancreas of larvae consists of a series of follicles residing in the connective tissue at the junction of the oesophagus and anterior intestine (Boenig 1927, 1928, 1929; Morris and Islam 1969). New follicles form throughout larval life (Keibel 1927; Ermisch 1966; Barrington 1972) and at metamorphosis the follicles are converted to cords of cells comprising a cranial pancreas. In addition, a caudal pancreas arises, partially embedded in the liver (Boenig 1927; Keibel 1927). The degenerating bile duct may contribute to the formation of the caudal pancreas (Boenig 1927). In *Geotria* no distinction is made between caudal and cranial portions of the pancreas (Maskell 1931). Metamorphosing *P. marinus* possess cranial and caudal portions of the pancreas as early as stage 1 (J. H. Youson unpublished data); therefore, the question of the origin and timing of development of this tissue remains questionable in this species.

Physiology

Some of the physiological and biochemical changes that take place at metamorphosis are directly related to, or are the result of, morphological transformation of tissues and organs. Other modifications cannot be equated to morphological transformation but are probably the direct result of the action of a triggering agent on specific genes. All changes, however, are related to preparing the adults for a different mode of activity in a different environment. There are few direct observations of physiological and biochemical modifications on metamorphosing specimens, although comparisons between ammocoetes and adults are numerous.

BLOOD

Early literature comparing the physiological and biochemical properties of the blood in larval and adult lampreys is provided by Manwell (1963). At the beginning of metamorphosis in *L. fluviatilis* and *L. planeri* (Potter and Brown 1975), in *M. mordax* (Potter and Nicol 1968), and in landlocked *P. marinus* (Beamish and Potter 1972) the electrophoretic pattern of hemoglobins is identical with that of ammocoetes. In *P. marinus* a mixed pattern of larval and adult hemoglobins is observed in metamorphosing specimens in late August and September but by late November the typical adult pattern is apparent (Beamish and Potter 1972). In contrast, *Lampetra* species show a much slower transformation of the hemoglobin pattern, despite the fact that metamorphosis begins at approximately the same time as in *P. marinus* (Potter and Brown 1975). There is also a slower rate of changeover in *L. planeri* than in *L. fluviatilis*.

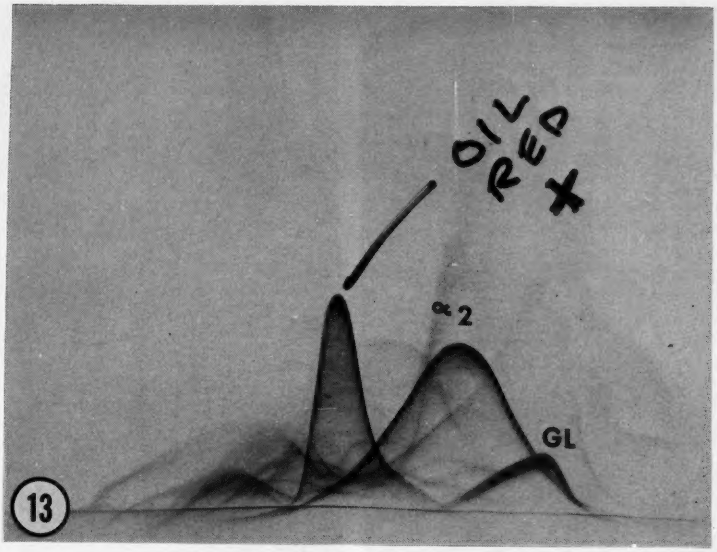
The initiation of metamorphosis in landlocked *P. marinus* in July is marked by a decrease in hematocrit (Beamish and Potter 1972). The hematocrit remains below that of ammocoetes and does not increase to the feeding adult level until the macrophthalmia stage (stage 7) in October (Beamish and Potter 1972). These trends may therefore be attributable to the destruction of erythrocytes containing larval hemoglobins and are followed later by the development of erythrocytes with adult hemoglobin.

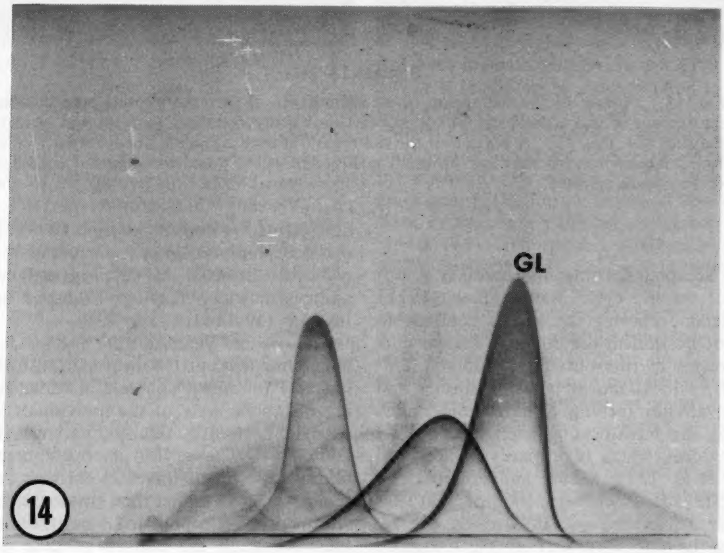
In landlocked *P. marinus* a significant increase in serum osmolarity marks the initiation of metamorphosis, and osmolarity continues to increase to the newly transformed adult stage (Mathers and Beamish 1974).

Changes in serum proteins in *P. marinus* at metamorphosis was first suggested by a study carried out on ammocoetes, newly transformed individuals, and mature adults (Rall et al. 1961). A component in adult plasma with a greater electrophoretic mobility than any seen in ammocoetes was designated as an α globulin. Albumin was not believed to be present in lamprey serum. Recent studies on anadromous sea lampreys have also shown quantitative differences in certain serum proteins of ammocoetes, metamorphosing animals, and adults (M. F. Filosa and J. H. Youson unpublished data). Using crossed immunoelectrophoresis with antiserum made in rabbits against serum from upstream migrants, the three major proteins are identified (Fig. 13) as a lipoprotein, a glycoprotein, and a protein corresponding to the α_2 globulin designated by Rall et al. (1961). In ammocoetes, the fastest moving component identified by Nagano et al. (1976) as a glycoprotein is variable in quantity and is occasionally absent, whereas the lipoprotein is represented as a broad, asymmetrical peak. At stage 1 the lipoprotein peak is symmetrical and narrow, the glycoprotein reveals the inconsistency of ammocoetes, and the α_2 globulin remains unchanged. The modification by stage 2 is that the glycoprotein is present in consistently greater amounts than in ammocoetes. Subsequent stages show a gradual slight increase in the height of the lipoprotein and glycoprotein peaks but no change in α_2 globulin (Fig. 14). In recently metamorphosed, young feeding adults, lipoprotein and α_2 globulin decreases in amount but the glycoprotein component greatly increases compared to all earlier stages.

OXYGEN CONSUMPTION

Later (stages 5 and 6) metamorphosing individuals of *Lampetra* spp. consume larger quantities of oxygen than ammocoetes and early metamorphosing specimens (Lewis and Potter 1977). The rather abrupt increase in oxygen consumption in the latter stages may parallel the tendency of the animals to remain unburrowed or attached by their suctorial disc, while they prefer to

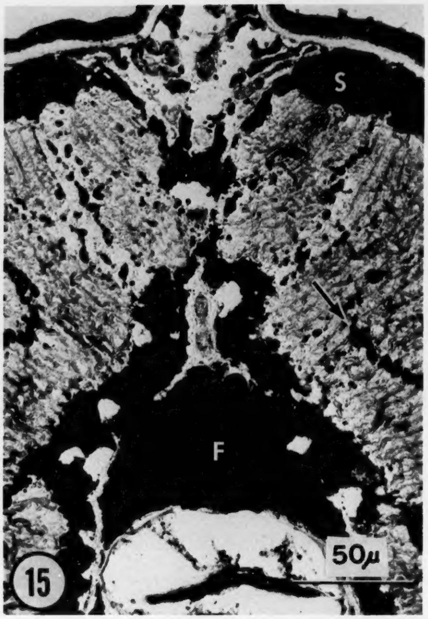


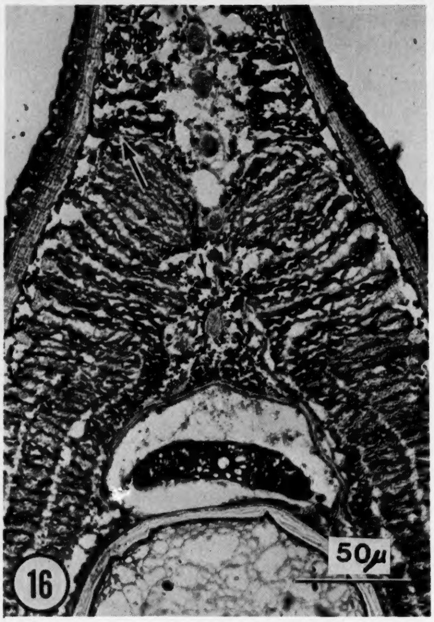


FIGURES 13–14

FIG. 13. Crossed immunoelectrophoresis of serum from a stage 1 animal reveals three primary proteins: lipoprotein (oil red +), α_2 globulin (α_2), and glycoprotein (GL). FIG. 14. Crossed immunoelectrophoresis of serum from a stage 3 animal showing that glycoprotein (GL) is present in greater amounts than in stage 1 (Fig. 13).

be burrowed at earlier stages (Lewis and Potter 1977). This information is in direct conflict with that provided by Leach (1946), who found no increase, and even perhaps a decline, in oxygen consumption during the metamorphosis of *I. fossor*. A detailed analysis of respiration is provided by Lewis (1980).





FIGURES 15–16

FIG. 15. Portion of the tail region of an ammocoete of metamorphosing size showing fat deposits in and around the fat column (F), in the myocommata (arrow) and beneath the skin (S). FIG. 16. A portion of the tail region of a young adult which recently completed metamorphosis showing the small quantity of fat (F) and the depleted condition of the muscle (arrow).

METABOLISM

It is generally accepted that metamorphosis is a nontrophic period of the life cycle. Poltorykhina (1971) believed that metamorphosing individuals continue to feed, but the modification to the digestive system during this phase seems to rule out this possibility. This period may last up to 10 mo in parasitic species and in nonparasitic varieties feeding is never undertaken again. Therefore, the transforming animals must rely on their energy stores, which is primarily in the form of lipid (Lowe et al. 1973; Moore and Potter 1976; Youson et al. 1979). In *P. marinus*, the principal sites of lipid storage are located in and around the fat column, lateral to the notochord, between the notochord and either the cardinal or caudal veins, surrounding the body cavity, beneath the skin, and in the myosepta and the nephric fold (Youson et al. 1979). The large quantities of fat present in large ammocoetes in May and June (Fig. 15) and in those animals in early stages of metamorphosis in July and August are believed to accumulate during the preceding autumn and winter months (Lowe et al. 1973). The gradual removal of this lipid from the storage sites has been thoroughly documented (Youson et al. 1979) throughout the metamorphic process in anadromous *P. marinus*. Complete exhaustion of this supply is only attained in those animals in which feeding is delayed until the following May (Fig. 16).

O'Boyle and Beamish (1977) have described changes in intermediary metabolism at transformation in landlocked *P. marinus*. The data provided reflects the existing metabolic state of the individuals at the time and does not necessarily signify differences in feeding larvae and adults. The serum glucose content of metamorphosing specimens increases through August and September to levels higher than ammocoetes. This coincides with a decline in both liver and muscle glycogen content. Although the pattern of liver enzyme changes during transformation appear to be simply a continuation of those processes initiated during the latter stages of "premetamorphosis," muscle enzymes, particularly hexose monophosphate shunt dehydrogenases and malic enzyme, increase in amount. Liver and muscle lipid declines but a complete shutdown of the liver lipogenic process is suggested (O'Boyle and Beamish 1977). A dramatic decline in both alkaline and acid phosphatase activity is reported in the liver of metamorphosing *L. planeri* (Buonanno and Chieffi 1965). In the adult, acid phosphatase activity rises to levels higher than in ammocoetes.

OSMOREGULATION

One of the important consequences of metamorphosis in anadromous species of lampreys is the ability to osmoregulate in saltwater during the parasitic phase (Morris 1972). In *P. marinus* the time at which this ability is acquired seems to be variable among the landlocked and the anadromous forms (Mathers and Beamish 1974; Beamish et al. 1978) in that the landlocked form must attain a larger size. No information is available on the osmoregulatory ability of metamorphosing anadromous *P. marinus*, but the landlocked variety cannot osmoregulate in even dilute saline solution until metamorphosis is complete. At this time they can tolerate 10‰ and have a serum osmolarity of 301 ± 2.5 mOsm/L (Mathers and Beamish 1974). If they are placed in this concentration during their period of transformation their serum osmolarity climbs from 227 ± 2.0 mOsm/L to 355 ± 2.4 mOsm/L in 1 d. The inability to cope with this salinity is undoubtedly because the kidneys, the gills, and the alimentary canal are not sufficiently developed towards their definitive adult form. For example, chloride cells of the gills are not fully differentiated until stages 6 and 7 in anadromous *P. marinus* (Peek and Youson 1979).

HORMONE LEVELS

Despite the importance of hormones in amphibian metamorphosis (Etkin 1968), little information on changes in levels of circulating and stored hormones is available for lampreys (Barrington 1968). Van de Kamer and Schreurs (1959) report a fall in amount of "neurosecretion" from the neurohypophysis of metamorphosing *L. planeri* but subsequently no parallel decline was observed in neurohypophysial peptides in *L. planeri* (Sterba 1961) or *L. richardsoni* (Rurak and Perks 1977). An increase in total oxytocic activity per animal at metamorphosis is probably a reflection of the growth of the neurohypophysial region (Rurak and Perks 1977).

Circulating levels of the thyroid hormone, thyroxine, drop drastically at the very onset of metamorphosis in anadromous *P. marinus* (Wright and Youson 1977). These levels remain much lower than those observed in ammocoetes throughout the remainder of the life cycle. The reason for the decline may be attributed to the inefficiency of the transforming endostyle, or the developing thyroid follicles, to synthesize thyroglobulin. However, the tissues of the transforming individuals and adults may also utilize and bind the circulating thyroxine more efficiently. It is also possible that thyroxine is more rapidly converted to the more biologically active tri-iodothyronine by the liver in these stages. The significance of this decline at metamorphosis remains to be elucidated.

Control of Metamorphosis

The factor(s) controlling lamprey metamorphosis are not known. As pointed out by Barrington (1968), it seems reasonable to assume that, as lampreys are vertebrates, the control is probably humoral (hormonal) or nervous. On the other hand, these factors probably act with environmental stimuli, such as temperature and light (Potter 1970; Purvis 1980). The literature contains numerous examples of attempts to initiate metamorphosis in ammocoetes through artificial means. These have been primarily concerned with the elements of the endocrine system.

The comprehensive investigation of Horton (1934) concludes that the thyroid gland has no significance to lamprey metamorphosis. Ammocoetes immersed in solutions containing either iodine, potassium iodide, or iodoform or those given thyroid extracts into the dorsal tail muscles do not metamorphose. Young and Bellerby (1935) obtained similar results by injecting anterior pituitary extracts of ox intraperitoneally into ammocoetes. Knowles (1939, 1941) found some internal changes in ammocoetes after injection of anterior pituitary extracts but the animals returned to normal form shortly after repeated injections. Extirpation of the endostyle does not retard metamorphosis (Sterba 1953) nor is it induced by thyroxine (Leach 1946). The view that there may be hypophysial control over metamorphosis (Sterba 1969; Falkmer et al. 1973) is suggested by the induction in ammocoetes of metamorphic changes in the endostyle with goitrogens (Sterba and Schneider 1961; Hoheisel and Sterba 1963; Barrington and Sage 1963a, b; Wright 1978) and thyrotrophin (Barrington 1972; Wright 1978). The goitrogen, potassium perchlorate, also induces external signs of metamorphosis in *L. planeri* (Hoheisel and Sterba 1963). The partial stimulation of metamorphosis by corticotrophin has also been reported (Sterba 1955).

Eddy (1969) provided experimental evidence to suggest that the pineal gland is involved in metamorphosis in *L. planeri*. This is based on the fact that no animals out of a total of 35 large pinealectomized ammocoetes underwent metamorphosis, whereas 7 of 20 controls (some sham and some unoperated) completed metamorphosis.

It is clear that until a method is available to determine which ammocoetes are certain to enter metamorphosis, little definitive information can be obtained from these experimental approaches.

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BALABAI, P. P. 1946. Metamorphosis of the visceral apparatus of the lamprey. Akad. Nauk SSSR, Leningr., C. R. (Dokl.) Acad. Sci. URSS, 53(8): 765–768.

Balabai, P. O. 1948. O Uremeni and Charaktere Tecennija Metamorphosa V. *Lampetra Mariae* Berg. Akad. Nauk. URSR Kiev. Inst. Zool. Trudy N.S. 1: 29–38.

Barrington, E. J. W. 1945. The supposed pancreatic organs of *Petromyzon fluviatilis* and *Myxine glutinosa*. Q. J. Microsc. Sci. 85: 391–417.

1968. Metamorphosis in lower chordates, p. 223–270. *In* W. Etkin and L. I. Gilbert [ed.] Metamorphosis. A problem in developmental biology. Appleton-Century-Crofts, New York.

1972. The pancreas and intestine, p. 134–169. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2. Academic Press, London and New York.

Barrington, E. J. W., and M. Sage. 1963a. On the responses of the glandular tracts and associated regions of the endostyle of the larval lamprey to goitrogens and thyroxine. Gen. Comp. Endocrinol. 3: 153–165.

1963b. On the responses of iodine-binding regions of the endostyle of the larval lamprey to goitrogens and thyroxine. Gen. Comp. Endocrinol. 3: 669–679.

Baxter, E. W. 1957. The development of the intestinal blood-system of lampreys (Petromyzonidae) with an account of the origin of vascular couples. Proc. Zool. Soc. Lond. 129: 371–396.

Baxter, E. W., and G. G. Robinson. 1942. The vascular couples of the hind-gut in the subclass Petromyzontia. Proc. Zool. Soc. Lond. 112: 138–146.

Beamish, F. W. H., and I. C. Potter. 1972. Timing of changes in the blood, morphology, and behavior of *Petromyzon marinus* during metamorphosis. J. Fish. Res. Board Can. 29: 1277–1282.

Beamish, F. W. H., P. D. Strachan, and E. Thomas. 1978. Osmotic and ionic performance of the anadromous sea lamprey, *Petromyzon marinus*. Comp. Biochem. Physiol. 60A: 435–443.

Bird, D. I., and I. C. Potter. 1979a. Metamorphosis in the paired species of lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). 1. A description of the timing and stages. J. Linn. Soc. London Zool. 65: 127–143.

1979b. Metamorphosis in the paired species of lampreys, *Lampetra fluviatilis* (L.), and *Lampetra planeri* (Block). 2. Quantitative data for body proportions, weights, lengths and sex ratios. J. Linn. Soc. London Zool. 65: 145–160.

Boenig, H. 1927. Studien zur Morphologie und Entwicklungsgeschichte des Pankreas beim Bachneunauge [*Lampetra* (*Petromyzon*) *planeri*] I. Teil. Z. Mikrosk.-Anat. Forsch. 8: 489–511.

1928. Studien zur Morphologie und Entwicklungsgeschichte des Pancreas beim Bachneunauge [*Lampetra* (*Petromyzon*) *planeri*] II. Teil. Z. Mikrosk.-Anat. Forsch. 12: 537–594.

1929. Studien zur Morphologie und Entwicklungsgeschichte des Pankreas beim Bachneunauge [*Lampetra* (*Petromyzon*) *planeri*]. III. Die Histologie und Histogenese des Pankreas. Z. Mikrosk.-Anat. Forsch. 17: 125–184.

Bowen, P. C. 1969. The cytology of the pronephros of lampreys, Ph.D. dissertation, Univ. Oxford, Oxford, UK. 184 p.

Bujor, M. P. 1890. Contribution à l'étude de la métamorphose l'ammocoetes branchialis en *Petromyzon planeri*. Rev. Biol. Nord Fr. 3E Année 8: 301–315.

1891a. Note préliminaire sur la métamorphose de l'ammocoetes branchialis en *Petromyzon planeri*. Rev. Biol. Nord Fr. 3E Année 1891: 201–212.

1891b. Contribution à l'étude métamorphose de l'ammocoetes branchialis en *Petromyzon planeri*. Rev. Biol. Nord Fr. 3E Année 9: 325–339.

1891c. Contribution à l'étude métamorphose de l'ammocoetes branchialis en *Petromyzon planeri*. Rev. Biol. Nord Fr. 3E Année 10: 365–390.

1891d. Contribution à l'étude métamorphose de l'ammocoetes branchialis en *Petromyzon planeri*. Rev. Biol. Nord Fr. 3E Année. 12: 474–486.

1891e. Contribution à l'étude métamorphose de l'ammocoetes branchialis en *Petromyzon planeri*. Rev. Biol. Nord Fr. 4E Année 2: 41–64.

Buonanno, C., and G. Chieffi. 1965. L'attivita delle fenilfosfatasi alcalina ed acida nel fegato di *Lampetra planeri* nel corso della metamorfosi. Accad. Naz. Lincei, Rome. Cl. Sci. Fis., Mat. Nat., Atti Rend., Ser 8, 38: 119–124.

Busson-Mabillot, S. 1967. Structure ovarienne chez la lamproie de planer adults, *Lampetra planeri* (Bloch). Arch. Zool. Exp. Gen. 108: 413–443.

Claridge, P. N., and I. C. Potter. 1974. Heart ratios at different stages in the life cycle of lampreys. Acta Zool. (Stockholm) 55: 61–69.

Damas, H. 1935. Contribution à l'étude de la métamorphose de la tête de la lamproie. Arch. Biol. (Paris) 46: 171–227.

1942. Le développement de la tête de la lamproie (*Lampetra fluviatilis* L.). Ann. Soc. R. Zool. Belg. 73.

Dawson, J. 1905. The breathing and feeding mechanism of the lampreys. I. Biol. Bull. 9: 21 p.

Dickson, D. H., and T. R. Collard. 1979. Retinal development in the lamprey (*Petromyzon marinus* L.): premetamorphic ammocoete eye. Am. J. Anat. 154: 321–336.

Downing, S. W., and R. R. Novales. 1971a. The fine structure of lamprey epidermis. I. Introduction and mucous cells. J. Ultrastruct. Res. 35: 282–294.

1971b. The fine structure of lamprey epidermis. 2. Club cells. J. Ultrastruct. Res. 35: 295–303.

1971c. The fine structure of lamprey epidermis. 3. Granular cells. J. Ultrastruct. Res. 35: 304–313.

Eddy, J. M. P. 1969. Metamorphosis and the pineal complex in the brook lamprey, *Lampetra planeri*. J. Endocrinol 44: 451–452.

1970. The structure and function of the pineal complex of *Lampetra* spp. Ph.D. thesis, Univ. of Wales, Wales, UK.

1972. The pineal complex, p. 91–103. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2. Academic Press, London and New York.

Eddy, J. M. P., and R. Strahan. 1970. The structure of the epiphysial complex of *Mordacia mordax* and *Geotria australis* (Petromyzonidae). Acta Zool. (Stockholm) 51: 67–84.

Ermisch, A. 1966. Beiträge zur Histologie und Topochemie des Inselsystems der Neunaugen unter Natülichen und experimentellen Bedingungen. Zool. Jahrb. Abt. Anat. Ontog. Tiere 83: 52–106.

Etkin, W. 1968. Hormonal control of amphibian metamorphosis, p. 313–348. *In* W. Etkin and L. I. Gilbert [ed.] Metamorphosis. A problem in developmental biology. Appleton-Century-Crofts, New York.

Falkmer, S., N. W. Thomas, and L. Boquist. 1973. Endocrinology of the Cyclostomata, p. 195–247. *In* H. Florkin and B. T. Scheer [ed.] Chemical zoology, Vol. 8, Primitive Deuterostomians, Cyclostomata, Fishes. Academic Press, New York and London.

Fange, R. 1972. The circulatory system, p. 241–259. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Academic Press, London and New York.

Freeman, P. A. 1974. The morphology of the gills at various stages in the life cycle of the Great Lakes lamprey, *Petromyzon marinus* (L). M.Sc. thesis, Univ. Toronto, Toronto, Ont. 130 p.

George, J. C., and F. W. H. Beamish. 1974. Haemocytology of the supraneural myeloid body in the sea lamprey during several phases of life cycle. Can. J. Zool. 52: 1585–1589.

Hansen, H. 1919. Anatomie und Entevicklung der Zyklostomenzähne unter Berücksihtigung iher phylogenetischen Stelling. Jena. Z. Med., Naturwiss. 56: 85–117.

Hansen, S. J., and J. H. Youson. 1978. Morphology of the epithelium in the alimentary tract of the larval lamprey, *Petromyzon marinus* L. J. Morph. 155: 193–217.

Hardisty, M. W. 1971. Gonadogenesis, sex differentiation and gametogenesis, p. 295–359. *In* M. W. Hardisty and I. C. Potter [ed.] The Biology of Lampreys, Vol. 1. Academic Press, London and New York.

Hardisty, M. W. 1972a. The interrenal, p. 171–192. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys, Vol. 2. Academic Press, London and New York.

Hardisty, M. W. 1972b. Quantitative and experimental studies on the interrenal tissues of the upstream migrant stage of the river lamprey, *Lampetra fluviatilis* L. Gen. Comp. Endocr. 18: 501–514.

Hardisty, M. W., and M. E. Baines. 1971. The ultrastructure of the cyclostome interrenal. Experientia 27: 1072–1075.

Hardisty, M. W., Potter, I. C., and Sturge, R. 1970. A comparison of the metamorphosing and macrophthalmic stages of the lampreys *Lampetra fluviatilis*, and *Lampetra planeri*. J. Zool. (Lond.) 162: 383–400.

Hatta, S. 1900. Contributions to the morphology of cyclostomata. II. On the development of the pronephros and segmental duct. J. Coll. Sci. Imp. Univ. Tokyo 13: 311–346.

Hatta, S. 1923. Über die Entwicklung des Getässystems des *Neunauges* (Lampetra mitsukurii *Hatta*). Zool. Jahrb. Abt. Anat. Ontog. Tiere 13: 1–88.

Healey, E. G. 1972. The central nervous system, p. 307–372. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2. Academic Press, London and New York.

Hoheisel, G., and G. Sterba. 1963. Über die Wirkung von Kaliumperchlorat (KClO$_4$) auf Ammocoeten von *Lampetra planeri*. Bloch. Z. Mikrosk.-Anat. Forsch. 70: 490–516.

Homma, S. 1978. Organization of the trigeminal motor nucleus before and after metamorphosis in lampreys. Brain Res. 140: 33–42.

Horton, F. W. 1934. On the relation of the thyroid gland to metamorphosis in the lamprey. J. Exp. Biol. 11: 247–261.

Imamura, Y. 1928. Beiträge zur Metamorphose des Beruchsorganes von *Petromyzon planeri*. Acta Med. Keijo 11: 1–22.

Johnels, A. G. 1948. On the development and morphology of the skeleton of the head of *Petromyzon*. Acta Zool. (Stockholm) 29: 139–279.

Johnels, A. G. 1950. On the dermal connective tissue of the head of *Petromyzon*. Acta Zool. (Stockholm) 31: 177–185.

Jordan, H. E., and C. C. Speidel. 1930. Blood formation in cyclostomes. Am. J. Anat. 216: 335–379.

Kaensche, C. C. 1890. Beiträge zur Kenntniss der Metamorphose des Ammöcoetes branchialis in *Petromyzon*. Zool. Beitr. 2: 219–250.

Keibel, F. 1927. Zur Entwicklungsgeschichte des vorderdarmes und des pankreas beim Bachneunauge [*Lampetra* (Petromyzon) *planeri*], und beim Flubneunauge [*Lampetra* (Petromyzon) *fluviatilis*]. Z. Mikrosk.-Anat. Forsch. 8: 408–476.

Kennedy, M. C., and K. Rubinson. 1977. Retinal projections in larval, transforming and adult sea lamprey, *Petromyzon marinus*. J. Comp. Neurol. 171: 465–480.

1978. The structure of the optic tectum in the sea lamprey, *Petromyzon marinus*. Anat. Rec. 190: 441–442.

Kleerekoper, H. 1972. The sense organs, p. 373–404. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2. Academic Press, London and New York.

Knowles, F. G. W. 1939. The influence of anterior-pituitary and testicular hormones on the sexual maturation of lampreys. J. Exp. Biol. 16: 535–547.

1941. The duration of larval life in ammocoetes and an attempt to accelerate metamorphosis by injections of an anterior-pituitary extract. Proc. Zool. Soc. Lond. Ser. A, 111: 101–109.

Kraentzel, F. 1933. Contribution à l'étude de la Lamproie fluviatile *Lampetra* (*Petromyzon*) *fluviatilis*, L. Arch. Biol. Paris 44: 469–517.

Larsen, L. O., and B. Rothwell. 1972. Adenohypophysis, p. 1–67. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2. Academic Press, London and New York.

Leach, J. W. 1946. Oxygen consumption of lampreys, with special reference to metamorphosis and phylogenetic position. Physiol. Zool. 19: 365–374.

Leach, W. J. 1939. The endostyle and thyroid gland of the brook lamprey, *Ichthyomyzon fossor*. J. Morphol. 65: 549–605.

1951. The hypophysis of lampreys in relation to the nasal apparatus. J. Morphol. 89: 217–255.

Lethbridge, R. C., and I. C. Potter. 1980. Quantitative studies on the skin of the paired species of lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). J. Morphol. 164: 39–46.

Lewis, J. C., and D. B. McMillan. 1965. The development of the ovary of the sea lamprey (*Petromyzon marinus* L.). J. Morphol. 117: 425–465.

Lewis, S. V. 1980. Respiration of lampreys. Can. J. Fish. Aquat. Sci. 37: 1711–1722.

Lewis, S. V., and I. C. Potter. 1976. Gill morphometrics of the lampreys *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). Acta Zool. (Stockholm) 57: 103–112.

1977. Oxygen consumption during the metamorphosis of the parasitic lamprey, *Lampetra fluviatilis* (L.) and its non-parasitic derivative, *Lampetra planeri* (Bloch). J. Exp. Biol. 69: 187–198.

Lohnisky, Y. 1967. Brook lamprey, *Lampetra planeri* (Bloch, 1784) from the basin of water reservoir Lipno of the River Itava. Cesk. Spol. Zool. Vestin 31: 170–178.

Lowe, D. R., F. W. H. Beamish, and I. C. Potter. 1973. Changes in the proximate body composition of the landlocked sea lamprey *Petromyzon marinus* (L.) during larval life and metamorphosis. J. Fish. Biol. 5: 673–682.

Lubosch, W. 1905. Die Entwicklung und Metamorphose des Geruchsorganes von Petromyzon und Sein Bedeutung für die Vegleichendl Anatomie des Geruchsorganes. Zena Z. Naturwiss. 40: 95–143.

Manion, P. J. 1972. Variations in melanophores among lampreys in the upper Great Lakes. Trans. Am. Fish. Soc. 101: 662–666.

Manion, P. J., and G. W. Piavis. 1977. Dentition throughout the life history of the landlocked sea lamprey, *Petromyzon marinus*. Copeia 4: 762–766.

Manion, P. J., and T. M. Stauffer. 1970. Metamorphosis of the landlocked sea lamprey, *Petromyzon marinus*. J. Fish. Res. Board Can. 27: 1735–1746.

Manwell, C. 1963. The blood proteins of cyclostomes. A study in phylogenetic and ontogenetic biochemistry, p. 372–455. *In* A. Brodal and R. Fange [ed.] The biology of myxine. Universitetsforlaget, Oslo, Norway.

Marine, D. 1913. The metamorphosis of the endostyle (thyroid gland) of the ammocoete branchialis (larval) land-locked *Petromyzon marinus* (Jordan) or *Petromyzon dorsatus* (Wilder). J. Exp. Med. 17: 379–395.

Marinelli, W., and A. Strenger. 1954. *Lampetra fluviatilis* (L.) Klasse Cyclostomata, p. 1–80. *In* Vergleichenden Anatomie und Morphologie der Wirbeltheire. Deuticke, Vienna.

Maskell, F. G. 1931. On the New Zealand lamprey, *Geotria australis* Gray. Part II. On the mid-gut diverticula, the bile duct, and the problem of the pancreas in the ammocoetes stage. N. Z. Inst. Trans. Proc. 61: 478–497.

1932. On the New Zealand lamprey, *Geotria australis* Gray. Part III. The loss of the mid-gut diverticula of the ammocoetes stage at metamorphosis. N. Z. Inst. Trans. Proc. 62: 120–128.

Mathers, J. S., and F. W. H. Beamish. 1974. Changes in serum osmotic and ionic concentration in landlocked *Petromyzon marinus*. Comp. Biochem. Physiol. 49A: 677–688.

Minelli, G., and M. C. Rossini. 1961. Struttere e Rapporti Vascolari Del Figato Nella Larva e Nell Adulto di Lampreda (*Lampetra planeri*). Arch. Ital. Anat. Embriol. 66: 384–406.

Moore, J. V., and I. C. Potter. 1976. Aspects of feeding and lipid deposition and utilisation in the lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch.). J. Anim. Ecol. 45: 699–712.

Morris, R. 1972. Osmoregulation, p. 193–239. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2. Academic Press, London and New York.

Morris, R., and D. S. Islam. 1969. The effect of hormones and hormone inhibitors on blood sugar regulation and the follicles of Langerhans in ammocoete larvae. Gen. Comp. Endocrinol. 12: 81–90.

Müller, A. 1856. On the development of lampreys. Ann. Mag. Nat. Hist. 18: 298–301.

Nagano, H., K. Hosaka, and R. Shukuya. 1976. The fastest migrating component of lamprey serum in zone electrophoresis. Comp. Biochem. Physiol. 54B: 369–374.

Nakao, T. 1977. Electron microscopic studies on the myotomes of larval lamprey, *Lampetra japonica*. Anat. Rec. 187: 383–404.

O'Boyle, R. N., and F. W. H. Beamish. 1977. Growth and intermediary metabolism of larval and metamorphosing stages of the landlocked sea lamprey, *Petromyzon marinus* L. Environ. Biol. Fish. 2: 103–120.

Ooi, E. C. 1977. Morphogenesis and growth of the opisthonephric kidney in the anadromous sea lamprey, *Petromyzon marinus* L., during larval development and metamorphosis. Ph.D. thesis, Univ. Toronto, Toronto, Ont. 184 p.

Ooi, E. C., and J. H. Youson. 1976. Growth of the opisthonephric kidney during larval life in the anadromous sea lamprey, *Petromyzon marinus* L. Can. J. Zool. 54: 1449–1458.

1977. Morphogenesis and growth of the definitive opisthonephros during metamorphosis of anadromous sea lamprey, *Petromyzon marinus* L. J. Embryol. Exp. Morphol. 42: 219–235.

1979. Regression of the larval opisthonephros during metamorphosis of the sea lamprey, *Petromyzon marinus* L. Am. J. Anat. 154: 57–79.

Paiement, J. M., and D. B. McMillan. 1975. The extracardiac chromaffin cells of larval lampreys. Gen. Comp. Endocrinol. 27: 495–508.

Parker, W. K. 1883. On the skeleton of the Marsipobranch. Part II. *Petromyzon*. R. Soc. Lond. Philos. Trans. 174: 411–457.

Peek, W. D., and J. H. Youson. 1979. Transformation of the interlamellar epithelium of the gills of the anadromous sea lamprey, *Petromyzon marinus* L., during metamorphosis. Can. J. Zool. 57: 1318–1332.

Percy, R., and I. C. Potter. 1976. Blood cell formation in the River Lamprey, *Lampetra fluviatilis*. J. Zool. (Lond.) 178: 319–340.

1977. Changes in haemopoietic sites during the metamorphosis of the lampreys, *Lampetra fluviatilis*, and *Lampetra planeri*. J. Zool. (Lond.) 183: 111–123.

1979. The intestinal blood circulation in the River Lamprey, *Lampetra fluviatilis*. J. Zool. (Lond.) 187: 415–431.

Percy, R., J. F. Leatherland, and F. W. H. Beamish. 1975. Structure and fine structure of the pituitary gland in the sea lamprey, *Petromyzon marinus* at different stages of its life cycle. Cell Tissue Res. 157: 141–164.

Peters, A., and B. MacKay. 1961. The structure and innervation of the myotomes of the lamprey. J. Anat. 95: 575–585.

Pfister, C. 1971. Die Matrixentwicklung in Mes — und Rhombenecephalon von *Lampetra planeri* (Bloch) (Cyclostomata) im Verlaufe des Individualzykus. J. Hirnforsch. 13: 377–383.

Poltorykhina, A. N. 1971. Metamorphosis of the Arctic brook lamprey [*Lampetra japonica kessleri* (Anikin)] in the Upper Irtysh. J. Ichthyol. 11: 281–285.

Potter, I. C. 1970. The life cycles and ecology of Australian lampreys of the genus *Mordacia*. J. Zool. (Lond.) 161: 487–511.

Potter, I. C., E. S. Robinson, and I. D. Brown. 1974. Studies on the erythrocytes of larval and adult lampreys (*Lampetra fluviatilis*). Acta Zool. (Stockholm) 55: 173–177.

Potter, I. C., G. M. Wright, and J. H. Youson. 1978b. Metamorphosis in the anadromous sea lamprey, *Petromyzon marinus* L. Can. J. Zool. 56: 561–570.

Potter, I. C., and I. D. Brown. 1975. Changes in haemoglobin electropherograms during the life cycle of two closely related lampreys. Comp. Biochem. Physiol. 51B: 517–519.

Potter, I. C., and P. A. Nicol. 1968. Electrophoretic studies on the haemoglobins of Australian lampreys. Aust. J. Exp. Biol. Med. Sci. 46: 639–641.

Potter, I. C., R. Percy, and J. H. Youson. 1978a. A proposal for the adaptive significance of the development of the lamprey fat column. Acta Zool. (Stockholm) 59: 63–67.

Purvis, H. A. 1980. Effects of temperature on metamorphosis and the age and length at metamorphosis in sea lamprey (*Petromyzon marinus*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1827–1834.

Rall, D. P., P. Schwab, and C. G. Zabrod. 1961. Alteration of plasma proteins at metamorphosis in the lamprey (*Petromyzon marinus dorsatus*). Science 133: 279–280.

Randall, D. J. 1972. Respiration, p. 287–306. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2. Academic Press, London and New York.

Rovainen, C. M. 1978. Müller cells, "Mauthner" cells, and other identified reticulospinal neurons in the lamprey, p. 245–269. *In* D. Faber and H. Korn [ed.] Neurobiology of the Mauthner cell. Raven Press, New York.

Rovainen, C. M., and K. L. Birnberger. 1971. Identification and properties of motoneurons to fin muscle of the sea lamprey. J. Neurophysiol. 34: 974–981.

Rurak, D. W., and A. M. Perks. 1977. The neurohypophysial principles of the western brook lamprey, *Lampetra richardsoni*: studies in the ammocoete larva. Gen. Comp. Endocrinol. 31: 91–100.

Schneider, A. 1874. Beiträge zur vergleichenden Anatomie und Entwicklungsgeschichte der Wirbelthiere Reimer, Berlin.

1879. Anatomie und Entwicklungsgeschichte von Petromyzon und Ammocoetes. Beit. Verg. Anat. Entwick. Wilber. Reimer, Berlin.

Schober, W. 1964. Vergleichend-anatomische Untersuchungen am Gehirn der Larven und adulten Tiere von *Lampetra fluviatilis* (Linné, 1758) und *Lampetra planeri* (Bloch, 1784). J. Hirnforsch. 7: 107–209.

Siebold, K. T. E. 1863. Die Süsswasserfische von Mitteleuropa, W. Engelmann, Leipzig. 430 p.

Seiler, K., and R. Seiler. 1973. Zur Topographie des Interrenal — und Adrenal — Systems des Bachneunauges (*Lampetra planeri* Bloch). Gegenbaurs Morph. Jahrb. (Leipzig) 119: 796–808.

Seiler, K., R. Seiler, and G. Sterba. 1970. Histochemische Untersuchungen am Interrenalsystem des Bachneunauges (*Lampetra planeri* Bloch). Acta Biol. Med. Ger. 24: 553–554.

Sognaees, R. F., and L. Lustig. 1955. Histochemical reactions of the lamprey mouth. J. Dent. Res. 34: 132–143.

Sterba, G. 1953. Die Physiologie und Histogenese der Schilddrüse und des Thymus beim Bachneunauge (*Lampetra planeri* Bloch = *Petromyzon planeri* Bloch) als Grundlagen phylogenetischer studien über die Evolution der innersekretorischen Kiemendarmderivate nebst einigen Mitteilugen über die Bionomie der Bachneunaugen und morphologische – physiologischen Untersuchungen über den, Kiel endarm. Wiss. Z. Friedrich-Schiller-Univ. Jena Math.–Naturwiss. Reihe 3: H2, 239–298.

1955. Das Adrenal — und Interrenalsystem im Lebensablauf von *Petromyzon planeri* Bloch. I. Morphologie und Histologie einschlieblich Histogenese. Zool. Anz. 155: 151–168.

1961. Fluoreszenzmikroskopische Untersuchungen über die Neurosekretion beim Bachneunauge (*Lampetra planeri* Bloch). Z. Zellforsch. Mikrosk. Anat. 55: 763–789.

1969. Endocrinology of the lamprey. Gen. Comp. Endocr. (Suppl.) 2: 500–509.

Sterba, G., and J. Schneider. 1961. Zur Wirkung von Kalium-perchlorat ($KClO_4$) auf Ammocoeten. Naturwissenschaften 48: 485–486.

Studnicka, F. K. 1893. Sur les organes parietaux de *Petromyzon planeri*. Sber. K. Böhm Ges. Wiss. 1893 (1): 1–50.

1899. Uber den feineren Bau der Parietalorgane von *Petromyzon marinus*. Sber K. Böhm Gesamten Wiss. 1899(37): 1–17.

1905. Die Parietalorgane, p. 12–44. *In* A. Oppel [ed.] Lehrbuch der Vergleichenden Mikroskopischen Anatomie der Wirbeltiere, Vol. 5. Fischer, Jena.

Teräväinen, H. 1971. Anatomical and physiological studies on muscles of lamprey. J. Neurophysiol. 34: 954–973.

Thompson, A. 1971. Quantitative and cytological studies on the adenohypophysis of *Lampetra planeri* and *Lampetra fluviatilis* with special reference to metamorphosis. M. Sc. thesis, Bath Univ., Bath, UK.

Thornhill, R. A. 1972. The development of the labyrinth of the lamprey (*Lampetra fluviatilis*, Linn. 1758). Proc. R. Soc. London Ser. B, 181: 175–198.

Trott, J. R., and R. Lucow. 1964. A macroscopic and microscopic investigation of the teeth of two cyclostomes. Acta Anat. 56: 201–215.

Van de Kamer, J. C., and A. F. Schreurs. 1959. The pituitary gland of the brook lamprey (*Lampetra planeri*) before, during, and after metamorphosis. (A preliminary, qualitative investigation) Z. Zellforsch. Mikrosk. Anat. 49: 605–639.

Vialleton, L. 1890. Développment post-embryonnaire du rein de l'ammocoete. C. R. Acad. Sci. Paris 111: 399–401.

Vladykov, V. D. 1950. Larvae of eastern American lampreys (Petromyzonidae) Naturaliste Can. 77: 73–94.

1960. Description of young ammocoetes belonging to two species of lampreys: *Petromyzon marinus* and *Entosphenus lamottenii*. J. Fish. Res. Board Can. 17: 267–288.

Wald, G. 1958. The significance of vertebrate metamorphosis. Science 128: 1481–1490.

Warren, E. 1902. On the teeth of *Petromyzon and Myxine*. Q. J. Microsc. Sci. 45: 631–636.

Weissenberg, R. 1925. Fluss und Bachneunauge (*Lampetra fluviatilis* L. und *Lampetra planeri* Bloch) ein Morphologisch-biologischer Vergleich. Zool. Anz. 63: 293–306.

1926. Beiträge zur Kenntnis der Biologie und Morphologie der Neunaugen. I. Vorderdarm und Mundbewaffnung bei *Lampetra fluviatilis* und *planeri*. Z. Mikorsk.-Anat. Forsch. 5: 153–184.

Wheeler, M. W. 1899. The development of the urogenital organs of the lamprey. Zool. Jahrb. Abt. Anat. Ontog. Tiere 13: 1–88.

Wright, G. M. 1978. The endostyle, thyroid, and metamorphosis in the anadromous sea lamprey, *Petromyzon marinus* L. Ph.D. thesis, Univ. Toronto, Toronto, Ont. 151 p.

Wright, G. M., and J. H. Youson. 1976. Transformation of the endostyle of the anadromous sea lamprey, *Petromyzon marinus* L., during metamorphosis. 1. Light microscopy and autoradiography with ^{125}I. Gen. Comp. Endocrinol. 30: 243–257.

1977. Serum thyroxine concentrations in larval and metamorphosing anadromous sea lamprey, *Petromyzon marinus* L. J. Exp. Zool. 202: 27–32.

Yamamoto, T. 1965. Some observations on the fine structure of the epithelium in the intestine of lamprey (*Lampetra japonica*). Okajimas Folia Anat. Jpn. 40: 691–713.

Young, J. Z., and C. W. Bellerby. 1935. The response of the lamprey to injection of anterior lobe pituitary extract. J. Exp. Biol. 12: 246–253.

Youson, J. H. 1970. Observations on the opisthonephric kidneys of the sea lamprey of the Great Lakes, *Petromyzon marinus* L., at various stages during the life cycle. Can. J. Zool. 48: 1313–1316.

1972. Structure and distribution of interstitial cells (presumptive interrenal cells) in the opisthonephric kidneys of larval and adult sea lamprey, *Petromyzon marinus* L. Gen. Comp. Endocrinol. 19: 56–68.

1973a. A comparison of presumptive interrenal tissue in the opisthonephric kidney and dorsal vessel region of the larval sea lamprey, *Petromyzon marinus* L. Can. J. Zool. 51: 796–799.

1973b. Effects of mammalian corticotrophin on the ultrastructure of presumptive interrenal cells in the opisthonephros of the lamprey, *Petromyzon marinus* L. Am. J. Anat. 138: 235–252.

Youson, J. H., and K. L. Connelly. 1978. Development of longitudinal mucosal folds in the intestine of the anadromous sea lamprey, *Petromyzon marinus* L., during metamorphosis. Can. J. Zool. 56: 2364–2371.

YOUSON, J. H., J. LEE, AND I. C. POTTER. 1979. The distribution of fat in larval, metamorphosing, and young adult anadromous sea lampreys, *Petromyzon marinus* L. Can. J. Zool. 57: 237–246.

YOUSON, J. H., AND D. B. MCMILLAN. 1970. The opisthonephric kidney of the sea lamprey of the Great Lakes. *Petromyzon marinus* L. II. Neck and proximal segments of the tubular nephron. Am. J. Anat. 127: 233–257.

1971a. The opisthonephric kidney of the sea lamprey of the Great Lakes, *Petromyzon marinus* L. IV. Intermediate, distal, and collecting segments of the adult. Am. J. Anat. 130: 281–303.

1971b. Intertubular circulation in the opisthonephric kidneys of adult and larval sea lamprey, *Petromyzon marinus* L. Anat. Rec. 170: 401–412.

YOUSON, J. H., AND E. C. OOI. 1979. Development of the renal corpuscle during metamorphosis in the lamprey. Am. J. Anat. 155: 201–222.

YOUSON, J. H., AND I. C. POTTER, 1979. A description of the stages in the metamorphosis of the anadromous sea lamprey, *Petromyzon marinus* L. Can. J. Zool. 57: 1808–1817.

YOUSON, J. H., AND E. W. SIDON. 1978. Lamprey biliary atresia: first model system for the human condition? Experientia 34: 1084–1086.

YOUSON, J. H., G. M. WRIGHT, AND E. C. OOI. 1977. The timing of changes in several internal organs during metamorphosis of anadromous larval lamprey, *Petromyzon marinus* L. Can. J. Zool. 55: 469–473.

Respiration of Lampreys[1]

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Lewis, S. V. 1980. Respiration of lampreys. Can. J. Fish. Aquat. Sci. 37: 1711–1722.

In lampreys, though the gross morphology of the branchial chamber and the method of ventilating the gills are radically different from that found in gnathostomes, the total gill area of larval (1462–2717 $mm^2 \cdot g^{-1}$) and adult (1402–2337 $mm^2 \cdot g^{-1}$) lampreys, the ultrastructure of the gills, and the thickness of the water–blood barrier are similar to active teleosts. The standard rates of oxygen consumption of ammocoetes are low, values for medium-sized *Ichthyomyzon hubbsi* ranging from 18.1 $\mu L \cdot g^{-1} \cdot h^{-1}$ at 3.5°C to 90.1 $\mu L \cdot g^{-1} \cdot h^{-1}$ at 22.5°C. The consumption rates increase during metamorphosis rising in *Lampetra fluviatilis* held at 10°C from 29.3 to 60.4 $\mu L \cdot g^{-1} \cdot h^{-1}$, and at the same time a circadian rhythm of consumption develops; maximum rates occur in the dark. Adult lampreys have consumption rates ranging from 66.1 $\mu L \cdot g^{-1} \cdot h^{-1}$ in *L. fluviatilis* to 36.9 $\mu L \cdot g^{-1} \cdot h^{-1}$ in *Petromyzon marinus*, and $Q10$'s in the temperature range 5–15°C are from 1.6 to 4.83. Sexually mature males of *L. planeri* and *L. fluviatilis* have higher metabolic rates than the females. The active oxygen consumption of *P. marinus* at 332.5 $\mu L \cdot g^{-1} \cdot h^{-1}$ is within the range reported for teleosts. Resting ventilation rates are higher in adults than ammocoetes and reach maximum values in sexually mature spawning males. Hypoxia results in an increase in the ventilation and heart rates.

Key words: lampreys, respiration; gills, morphology; oxygen consumption, sexual maturity, ventilation rates

Lewis, S. V. 1980. Respiration of lampreys. Can. J. Fish. Aquat. Sci. 37: 1711–1722.

Bien que la morphologie macroscopique de la chambre branchiale et la méthode de ventilation des branchies des lamproies soient radicalement différentes de celles des gnathostomes, la superficie totale des branchies des larves (1462–2717 $mm^2 \cdot g^{-1}$) et des lamproies adultes (1402–2337 $mm^2 \cdot g^{-1}$) ainsi que la structure fine des branchies et l'épaisseur de la barrière eau–sang sont semblables à celles des téléostéens actifs. Les taux normaux de consommation d'oxygène des ammocètes sont faibles, les valeurs chez *Ichthyomyzon hubbsi* de taille moyenne s'étalant de 18,1 $\mu L \cdot g^{-1} \cdot h^{-1}$ à 3,5°C à 90,1 $\mu L \cdot g^{-1} \cdot h^{-1}$ à 22,5°C. Les taux de consommation augmentent durant la métamorphose, passant, chez *Lampetra fluviatilis* maintenue à 10°C, de 29,3 à 60,4 $\mu L \cdot g^{-1} \cdot h^{-1}$, alors qu'en même temps s'établit un rythme circadien de consommation; les taux maximaux se produisent à la noirceur. Les lamproies adultes ont des taux de consommation allant de 66,1 $\mu L \cdot g^{-1} \cdot h^{-1}$ chez *L. fluviatilis* à 36,9 $\mu L \cdot g^{-1} \cdot h^{-1}$ chez *Petromyzon marinus*, et les $Q10$ dans la gamme des températures de 5 à 15°C varient de 1,6 à 4,83. Les mâles de *L. planeri* et *L. fluviatilis* sexuellement mûrs ont des taux métaboliques supérieurs à ceux des femelles. La consommation d'oxygène en activité au taux de 332,5 $\mu L \cdot g^{-1} \cdot h^{-1}$ se situe dans la gamme signalée chez les téléostéens. Les taux de ventilation au repos sont plus élevés chez les adultes que chez les ammocètes et atteignent des valeurs maximales chez les mâles en voie de fraie sexuellement mûrs. L'hypoxie mène à une augmentation des taux de ventilation et de battement de coeur.

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AGNATHANS differ markedly from gnathostomes in the position of their branchial skeleton. Thus, whereas the skeleton lies outside the gills in the cyclostomes and in the fossil agnatha, it is located inside the gills in the "jawed" fishes. In fact, the orientation of the gills in the precursors of the gnathostomes is seen as having been a major factor in permitting the evolution of biting jaws (Jarvik 1964, 1968; Stensiö 1968). It has even been suggested that the inward-facing gills of the agnathans actually prevented the development of jaws and thereby limited the feeding strategies available to the group (Moy-Thomas 1971; Stahl 1974).

Considerable progress has been made in relating the morphology of the gills of different teleosts to both their mode of life (Hughes and Morgan 1973) and their rate of oxygen consumption (Hughes 1978). For example, the surface area of the gills of teleosts is greatest in the more active species (Hughes 1966; Hughes and Morgan 1973), a feature presumably related to their greater oxygen requirements (Hughes 1978). Furthermore, correlations have been found be-

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tween the size and number of the components of the gill system and the degree of activity of the species. For example, the secondary lamellae tend to be smaller, more numerous, and more closely packed in the more motile species (Hughes and Gray 1972). Recent ultrastructure studies have indicated that the water–blood barrier of the secondary lamellae tends to be thinner in active teleosts (Hughes 1970; Hughes and Morgan 1973), which presumably permits a more rapid transfer of gases between water and blood (Hughes 1978).

Measurements of oxygen consumption in teleosts have in recent years usually involved a respirometer containing a chamber in which the fish can swim (e.g. Farmer and Beamish 1969; Brett 1973). This has enabled workers to measure oxygen consumption rates during activity and to estimate those of inactive animals. These latter values, known as the standard rate of oxygen consumption (Beamish and Mookherji 1964), have also been obtained by monitoring oxygen consumption during periods when the fish are inactive, but the feasability of this type of measurement depends to a large extent on the behavioral characteristics of the species.

One of the great advantages of studying oxygen consumption in lampreys is that, under certain conditions, both the larvae and adults will settle down and exhibit little or no movement for prolonged periods. This enables the standard rate of oxygen consumption to be measured directly during both main stages in the life cycle.

In this review, comparisons are made both between lampreys and teleosts and between ammocoetes and adult lampreys. Emphasis has been placed on morphology, ultrastructure, size, and method of irrigating the gills and on the standard and active rates of oxygen consumption.

BRANCHIAL CHAMBER

The morphology of the branchial chamber of both larval and adult lampreys has been described by a number of workers (Dawson 1905; Roberts 1950; Sterba 1953; Randall 1972). The main differences in the arrangement of the gills can be related to differences in the methods of feeding and ventilation. The larva maintains a unidirectional flow of water over the gills, this entering the pharynx through the oral hood and passing out via the external branchiopores. This flow serves not only a respiratory function but is also responsible for carrying into the pharynx the microorganisms and detritus that form the basis of the animal's food (Creaser and Hann 1929; Schroll 1959; Moore and Potter 1976). In contrast to the situation in ammocoetes, the gills of the adult are ventilated by a tidal flow of water which passes both in and out through the branchiopores. The adult mechanism is clearly an adaptation to enable the animal to ventilate its gills while remaining attached for long periods to its host. The fundamental difference between the anatomical arrangement of the respiratory apparatus in ammocoetes and adults is that in the latter stage in the life cycle the gills have become enclosed in a series of pouches with only an indirect access to the central part of the pharynx (Fig. 1).

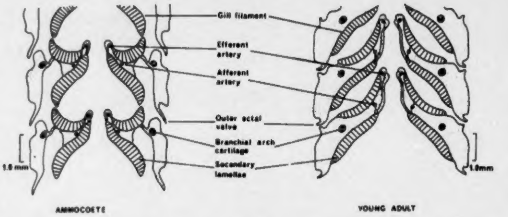

FIG. 1. Arrangement of the gills in an ammocoete and a young adult of *Lampetra fluviatilis* as seen in median horizontal section (Lewis and Potter 1976a).

Gill structure and area — Despite the differences in the arrangement of the gills within the branchial chamber of larvae and adults, the secondary lamellae of the gills are borne on the gill filaments in essentially the same manner (Fig. 2) and are of comparable shape in both life cycle stages (Lewis and Potter 1976a). Each lamella thus extends at right angles from the axis of the supporting gill filaments, which themselves lie parallel to each other (Lewis and Potter 1976b).

Estimates of the total area of the gills of lampreys have produced conflicting results. Sterba (1953) estimated the gill area of a 3.5-g adult *Lampetra planeri* to be 150 $\mathrm{mm}^2 \cdot \mathrm{g}^{-1}$, while Czopek and Sawa (1971) reported a value of 260 $\mathrm{mm}^2 \cdot \mathrm{g}^{-1}$ for a 70-g adult of *L. fluviatilis*. These values are small compared with those of most teleosts (Randall 1972; Hughes and Morgan 1973). However, a study made on larval, metamorphosing, and adult stages of *L. fluviatilis* and *L. planeri* by Lewis and Potter (1976a) suggested that the gill areas of lampreys are comparable with even the

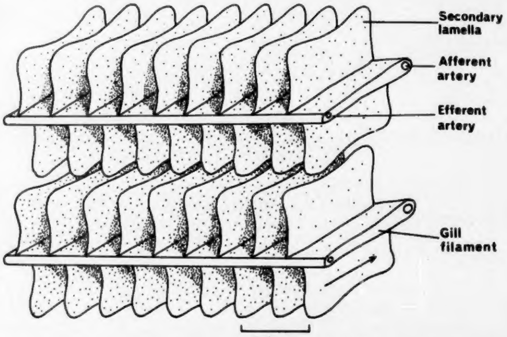

FIG. 2. Arrangement of secondary lamellae on the gill filaments found in all stages in the life cycle of *Lampetra* species (Lewis and Potter 1976a).

most active teleosts (Hughes and Morgan 1973). Thus, the total gill area of 1402–2337 $mm^2 \cdot g^{-1}$ found in *L. fluviatilis* weighing between 16.7 and 79.8 g is similar to those recorded for such active fish as the skipjack, *Katsuwonus pelamis*, and the perch-pike, *Lucioperca lucioperca* (Byczkowska-Smyk 1958; Muir and Hughes 1969). Even the sedentary ammocoetes of between 0.24 and 4.06 g have gill areas ranging from 1462 to 2717 $mm^2 \cdot g^{-1}$ (Lewis and Potter 1976a). It is possible that the values recorded by Sterba and by Czopek and Sawa were low because of their methodology and to the sequence of treatments their animals received. The logarithmic regression for the relationship between total gill area and body weight of *L. fluviatilis* yielded slopes of 0.860 in the case of ammocoetes and 0.899 for adults (Lewis and Potter 1976a). These are similar to those recorded for teleosts (Muir and Hughes 1969; Hughes and Gray 1972).

Although there are no major changes in the total gill area during metamorphosis, which is surprising since the young adults are more active than ammocoetes, there are changes in the individual components that contribute to the total gill area (Lewis and Potter 1976a). For example, an increase occurs in the total number of filaments, in the total length of the filaments, and in the number of secondary lamellae per unit length of filament, all of which contribute to an increase in the total number of secondary lamellae. In contrast, a decrease takes place in the average bilateral area of the individual secondary lamellae. The smaller area of the individual secondary lamellae, together with a reduction in the spacing between lamellae developed during metamorphosis, parallels differences found between active and less motile teleosts (Hughes and Morgan 1973).

Surface structure of the gills — The efficiency of gaseous exchange in aquatic organisms depends to some extent on the interaction between the flow of water and the surface of the respiratory organ. For this reason, it is important to examine the structure of the surface of the secondary lamellae, a process that can best be achieved by using the scanning electron microscope.

A prominent feature of the secondary lamellae of lampreys is that they are covered by an extensive network of microridges (Fig. 3 and 4) (Lewis and Potter 1976b) similar to those described for a number of teleosts (Olson and Fromm 1973; Rajbanshi 1977; Hughes 1979). The precise function of these surface projections is not clear. However, it might be significant that they increase the surface area of the secondary lamellae of trout gills by a factor of 2.5 (Olson and Fromm 1973) and in *L. fluviatilis* by 1.8 (Lewis and Potter 1976b). Whether or not this increase in surface area would significantly effect the amount of gaseous exchange is not known. Moreover, it has been claimed that a layer of mucus normally covers the lamellae (Hughes and Wright 1970), which means that the surface presented to the respiratory water would be the same as if there were no microridges. However, this thick layer of mucus may be an artifact of fixation (Olson and Fromm 1973; Lewis and Potter 1976b), and the microridges may normally project into the path of the water flow causing a very localized region of turbulence close to the lamellar surface (Lewis and Potter 1976b). Because the thin layer of "stagnant" water next to the lamellar surface (in a laminar flow between the secondary lamellae) is a major barrier to gaseous diffusion (Hills and Hughes 1970), any structure, such as microridges, which would help to mix oxygenated and "stagnant" water would be advantageous to the animal (Lewis and Potter 1976b; Hughes 1978). A further possible function of the microridges is that when the gills are exposed to potentially harmful effects they may help to anchor the mucus which is produced at such times and which may form an important protective barrier. Finally, the microridges may be formed as a result of the action of the water flow on the cell surfaces (Hughes 1979).

Ultrastructure of the gills — Many of the ultrastructural studies on the gills of lampreys have been on the cells involved in ion regulation and transport (Morris and Pickering 1975; 1976; Pickering and Morris 1976; 1977; Nakao 1974; Nakao and Uchinomiya 1974). Studies on the ultrastructure of the secondary lamellae indicate that these components of the gills of *P. marinus* (Youson and Freeman 1976) are similar to *L. fluviatilis* (Lewis 1976), though differences occur between the gills of larval and adult lampreys.

The secondary lamellae of lampreys have similar ultrastructural characteristics to those described for teleosts. The lamella consist of an outer epithelium two cells thick and central pillar cell bodies; flanges extend outwards from the pillar cell bodies and join and enclose the central blood space, except at the marginal channel where the lining consists of endothelial cells. Bundles of collagen fibers extend from spaces within the pillar cell bodies to the basement membrane with which they fuse to form a continuous layer around the lamellae beneath the epithelium. This latter arrangement is similar to that described for the gills of elasmobranchs and teleosts, in which it is said to help maintain the structural integrity of the lamellae (Hughes and Morgan 1973). However, in lampreys the pillar cells are randomly distributed whereas in teleosts, in which the blood flow within the lamellae is believed to be laminar (Hughes and Wright 1970; Hughes and Morgan 1973), they often form a parallel or even arrangement.

A major difference between the lamellae of different stages in the life cycle of lampreys is that intercellular spaces are abundant in the epithelium of the larvae but much reduced in the adult. The presence of large intercellular spaces are a feature of the developing gills of young trout and may be absent in adult fish (Morgan 1974).

The thickness of the water–blood barrier varies both

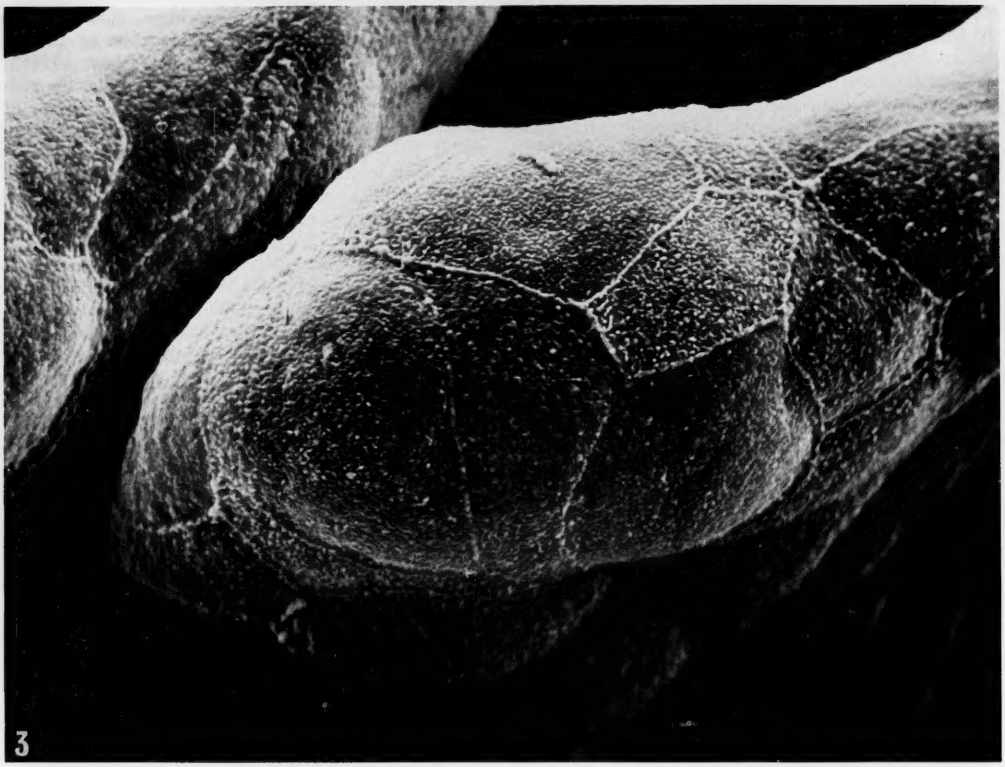

FIG. 3. Scanning electron micrograph (SEM) of the leading edge of a secondary lamella showing the raised boundaries between surface epithelium cells in an adult *L. fluviatilis*. Original × 1800. (from Lewis and Potter 1976b).

during each life cycle stage and between larva and adult (Lewis 1976). Thus during larval life in *L. planeri*, the thickness declined with increasing body weight with values of 6.25 μm being recorded for a 0.25-g ammocoete compared with 2.59 μm for a 3.0-g animal. After the completion of metamorphosis, the thickness fell to 1.95 μm for a 3.62-g adult *L. planeri*, this reduction in barrier thickness paralleling the differences found between sedentary and active gnathostomatous fishes (Hughes and Morgan 1973). Presumably, this reflects the fact that a more active species or life cycle stage has greater oxygen requirements and would tend to have thinner tissue barriers separating the water and blood. However, the barrier thickness increases with body weight in adult lampreys, as it also does in teleost fishes (Hughes 1972), a situation which probably reflects the greater tissue layer required for supporting the larger secondary lamellae of heavier animals.

The diffusion capacity of the tissue component of the gills, D_t, has been used as an estimate of the efficiency of these gaseous exchange organs (Hughes 1972). It is derived from a modification of the Fick equation, $D_t = KA/t$ where K is Krogh's permeation constant, A is the total gill area, and t is the tissue thickness. In lampreys, the logarithmic relationship between D_t and body weight is linear with a slope of 0.86 in larvae and 0.89 in adults (Lewis 1976). The absolute value of D_t varies between 68.38 and 245.00 mL $O_2 \cdot min^{-1} \cdot Pa^{-1} \cdot kg^{-1}$ recorded for a 925-g adult *P. marinus* and a 3.62-g adult *L. planeri*, respectively, values which are similar to those calculated for teleosts (Hughes and Morgan, 1973). A value of 97.31 mL $O_2 \cdot min^{-1} \cdot Pa^{-1} \cdot kg^{-1}$ calculated for a "standard" 100-g lamprey (Lewis 1976) is comparable to values calculated for very active teleosts, such as *K. pelamis* and *Trachurus trachurus* (Hughes and Morgan 1973).

SKIN

Although gaseous exchange probably occurs across the skin of ammocoetes (Rovainen and Schieber

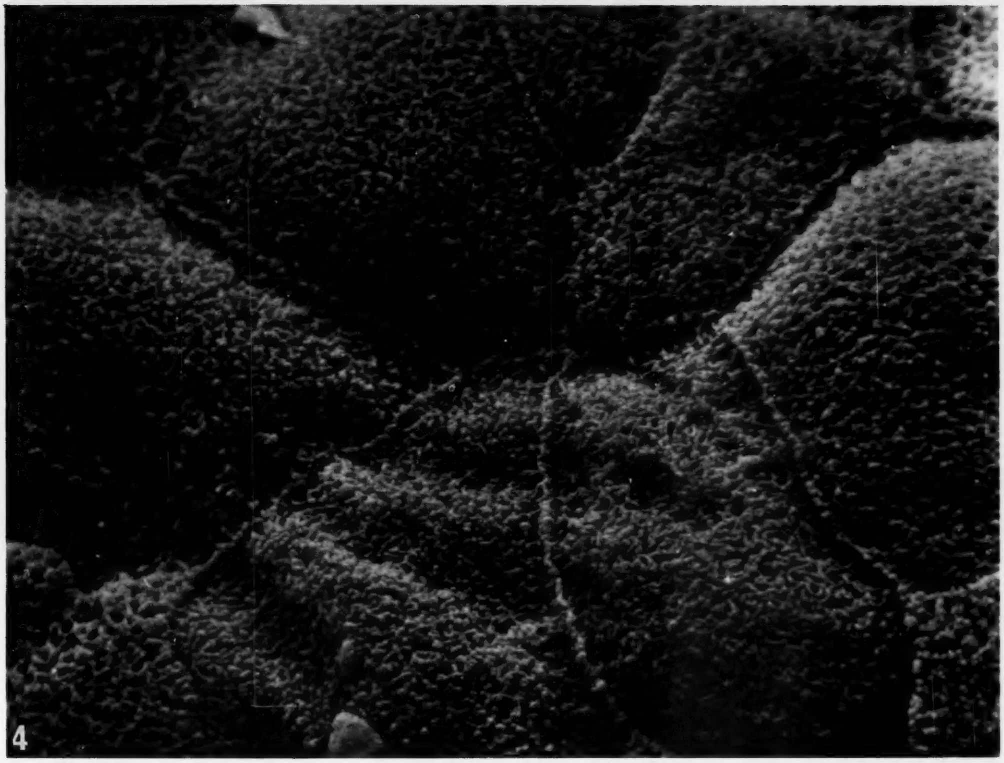

FIG. 4. SEM of the surface of the secondary lamella of an adult *L. fluviatilis* revealing the microridges. Original × 3000 (from Lewis and Potter 1976b).

1975), no measurements of cutaneous respiration have been reported for this stage in the life cycle. For adult *L. fluviatilis* Korolewa (1964) calculated that at 5–10°C, between 10.4 and 32.6% of the oxygen requirements were due to cutaneous respiration, while Czopek (1970) concluded that respiration through the skin of adults of the same species was negligable since animals prevented from using their gills died within 6 h.

The thickness of the epidermis of the skin of adult river lampreys varies between 120 and 260 μm (Czopek and Sawa 1971), the latter measurement being similar to the 250–300 μm recorded for *Ichthyomyzon unicuspis* (Downing and Novales 1971). These values are similar to the eel (*Anguilla anguilla*) or pond loach (*Misqurnis fossilis*), both of which can obtain a high proportion of their oxygen through the skin (Czopek and Sawa 1971). The thickness is substantially lower in ammocoetes for which values of 70 μm have been recorded for most of the body of *I. unicuspis*, with lower values of 35 μm being given for the fins, tail, and ventral part of the body (Downing and Novales 1971).

OXYGEN CONSUMPTION

Larvae — The importance of providing a suitable substrate into which ammocoetes can burrow for obtaining standard rates of oxygen consumption has been demonstrated by Potter and Rogers (1972). In this study, unburrowed ammocoetes of *L. planeri* consumed oxygen at a rate of 41.7 μL·g^{-1}·h^{-1} compared with 69.0 μL·g^{-1}·h^{-1} in burrowed ammocoetes under otherwise identical conditions. Moreover, while the burrowed larvae took only 3 h for the consumption rates to fall to a relatively constant level, 12 h was required in the case of unburrowed animals (Potter and Rogers 1972). It is almost certain that the high consumption rates recorded for larval *I. fossor* and *P. marinus* by Leach (1946) are due to his experimental conditions rather than to interspecific differences, since the animals were not provided with a substrate.

The metabolic rate of burrowed larval lampreys is low compared with teleosts of comparable size. In *L. planeri*, oxygen consumption rates of 41.7 μL·g^{-1}·h^{-1} in the light and 40.1 μL·g^{-1}·h^{-1} in the dark have been

TABLE 1. Equations relating oxygen consumption to body weight where Y represents oxygen consumption in $\mu L \cdot h^{-1}$ and X represents body weight in grams.

Species	Temp. (°C)	Sample size	Mean wt (g)	(Range)	
P. marinus[a] (adults)	5	20	22.8	(5.2–92.0)	$\log Y = -4.298+0.933 \log X$
	10	17	34.8	(6.8–100.0)	$\log Y = -4.277+0.966 \log X$
	15	19	35.7	(9.0–139.8)	$\log Y = -3.996+0.949 \log X$
	20	9	75.6	(36.0–137.7)	$\log Y = -3.960+0.949 \log X$
L. fluviatilis[b] (adults)	5	5			$\log Y = -4.988+1.002 \log X$
	9.5	21	46.8	(21.4–78.1)	$\log Y = -4.142+0.912 \log X$
	16	10			$\log Y = -3.848+0.925 \log X$
I. hubbsi[c] (larvae)	15.5	57		(0.11–4.71)	$\log Y = 1.735+0.718 \log X$
L. planeri[d] (larvae)	15	20	1.34	(0.64–2.07)	$\log Y = 1.623+0.780 \log X$

[a]From Beamish (1973).
[b]From Claridge and Potter (1975).
[c]From Hill and Potter (1970).
[d]From Rogers (1971) and Potter and Rogers (1972).

recorded at 15°C for animals whose mean weight was ~1.3 g (Potter and Rogers 1972). Although a higher rate of oxygen consumption ($58.0\, \mu L \cdot g^{-1} \cdot h^{-1}$) has been recorded for *L. fluviatilis* at the same temperature, the values are still relatively low.

Care must be taken in comparing ammocoetes of different weights, since the slope of the logarithmic regression line relating oxygen consumption and body weight is less than unity (Table 1). For example, a slope of 0.718 was recorded by Hill and Potter (1970) for *I. hubbsi* ranging in weight from 0.1 to 4.71 g, a value similar to 0.780 calculated for *L. planeri* ammocoetes (Potter and Rogers 1972). In contrast to these findings, however, Bourque (1970) was unable to find a change in the rate of oxygen consumption with increasing weight in the case of ammocoetes of *L. japonica.*

The oxygen uptake of ammocoetes varies considerably with changes in temperature (Table 2). For example, consumption by larval *L. fluviatilis* rose from about $11\, \mu L \cdot g^{-1} \cdot h^{-1}$ at 5°C to $29.3\, \mu L \cdot g^{-1} \cdot h^{-1}$ at 10°C, representing a *Q*10 of 7.26 (Lewis and Potter 1977). Over higher temperature ranges, the *Q*10 is generally much lower, a value of 2.2 being recorded for larvae of *I. hubbsi* over the range 15.5–22.5°C (Hill and Potter 1970).

No data are available on the oxygen consumption of ammocoetes exposed to hypoxia.

Metamorphosis — As mentioned previously, the branchial chamber undergoes extensive modifications during metamorphosis, a process that permits the development of a different method of gill ventilation. These morphological changes are accompanied by alterations in the behavior of the animal. Before metamorphosis, the larvae of lampreys spend most of their time burried in a substrate. Laboratory experiments have shown that by the completion of metamorphosis (stage 6), both *L. fluviatilis* and *L. planeri* spend less than 40% of their time burrowed (Lewis and Potter 1977). Moreover, as the oral disk becomes functional the lamprey spends an increasing amount of time attached to the side of the experimental chamber. The concomitant development of functional lateral eyes is associated with the appearance of a circadian rhythm of activity in which the animals are most active in the dark (Lewis and Potter 1977).

The rate of oxygen consumption increases during metamorphosis of both *L. planeri* and *L. fluviatilis* (Table 3), with the rates in both species having risen to levels at least twice that of larvae of comparable weight by stage 6 (Lewis and Potter 1977). Thus at 10°C, the rates in *L. planeri* rose from 20.3 to 50.5 $\mu L \cdot g^{-1} \cdot h^{-1}$ and in *L. fluviatilis* from 29.3 to 60.4 $\mu L \cdot g^{-1} \cdot h^{-1}$ (Fig. 5). This contrasts with the situation found by Leach (1946) in the early stages of metamorphosis in *I. fossor.* The probable explanation for this contrast lies in a combination of the fact that Leach did not provide a substrate for the animals and that the early metamorphosing stages are less active than ammocoetes.

Paralleling activity patterns, a circadian rhythm of standard oxygen consumption develops in *L. fluviatilis* by stage 6 of metamorphosis with maximum rates being attained in the dark (Lewis and Potter 1977).

Adults — Considerable variation exists in the values given for the oxygen consumption rates of the adult stage of different species of lampreys (Table 4). For example, at 5°C values of $21.2\, \mu L \cdot g^{-1} \cdot h^{-1}$ have been recorded for the Pacific lamprey *Entosphenus tridentatus* (Johansen et al. 1973), $36.9\, \mu L \cdot g^{-1} \cdot h^{-1}$ for *P. marinus* (Beamish 1973), and $10.5\, \mu L \cdot g^{-1} \cdot h^{-1}$ for *L. fluviatilis* (Claridge and Potter 1975). It seems likely that these differences are not solely due to interspecific differences but rather to differences in the ac-

TABLE 2. The $Q10$ for oxygen consumption, ventilatory, and heart rate for a number of lamprey species.

Species	Temp. range (°C)	Oxygen consumption	Ventilatory frequency	Heart rate
P. marinus[a] (adults)	5.0–10.0	1.5	—	—
	10.0–15.0	3.1	—	—
	15.0–20.0	1.18	—	—
	5.0–20.0	1.80	—	—
L. fluviatilis[b] (adults)	5.0–9.5	7.73	2.17	1.82
	9.5–16.0	3.48	2.13	1.44
	5.0–16.0	4.83	2.15	1.59
E. tridentatus[c] (adults)	5.0–15.0	1.6	—	—
	15.0–20.0	6.0	—	—
	5.0–20.0	2.65	—	—
I. hubbsi[d] (larvae)	3.5–9.5	5.4	—	—
	9.5–15.5	4.0	—	—
	15.5–22.5	2.2	—	—
	3.5–22.5	3.6	—	—
L. fluviatilis[e] (larvae)	5.0–10.0	7.26	—	—
	10.0–15.0	3.85	—	—
	5.0–15.0	5.29	—	—
Stage 6	5.0–10.0	6.18	3.09	—
	10.0–15.0	2.95	2.83	—
	5.0–15.0	4.24	2.96	—
L. planeri[e] (larvae)	5.0–10.0	6.41	—	—
	10.0–15.0	4.76	—	—
	5.0–15.0	5.51	—	—
Stage 6	5.0–10.0	5.60	2.09	—
	10.0–15.0	2.28	2.64	—
	5.0–15.0	3.57	2.35	—

[a] From Beamish (1973).
[b] From Claridge and Potter (1975).
[c] From Johansen, et al. (1973).
[d] From Hill and Potter (1970).
[e] From Lewis and Potter (1977).

climation and experimental regimes, trophic state of the animal, size, sex, and degree of sexual maturity.

The regression coefficients for the logarithmic relationship between oxygen consumption and body weight for adults are consistently higher than those of ammocoetes (Table 1) and may approach unity. There are considerable differences in the degree of change in oxygen consumption between species and between different temperature regimes (Table 2). $Q10$'s of 1.6 have been calculated for *E. tridentatus* between 5 and 15°C (Johansen et al. 1973) and of 1.8 for *P. marinus* between 5 and 20°C Beamish 1973), in contrast to $Q10$'s of 4.83 and 3.57 that have been recorded for adult *L. fluviatilis* (Claridge and Potter 1975) and young adult *L. planeri* (Lewis and Potter 1977) over a similar temperature range.

With the approach of sexual maturity, the upstream migrating adults of the river lamprey, *L. fluviatilis*, increase their rate of oxygen consumption (Fig. 6). Thus, in November at the start of the migration, the consumption rate at 9.5°C was 26.6 $\mu L \cdot g^{-1} \cdot h^{-1}$ but by the beginning of April had reached 48.2 $\mu L \cdot g^{-1} \cdot h^{-1}$ (Claridge and Potter 1975). This is almost certainly partly related to the change in hormone levels that occur during the period of maturation (e.g. Barnes and Hardisty 1972).

A circadian rhythm of activity, in which the animal is more active at night, is displayed by upstream migrating lampreys. In *L. fluviatilis*, this is reflected by a higher rate of oxygen consumption during nocturnal activity and is paralleled by an increase in the standard rate of consumption during the night (Claridge and Potter 1975). A similar situation is also found in young adults of the nonparasitic lamprey, *L. planeri* (Lewis and Potter 1977).

A marked sexual dimorphism in oxygen uptake is exhibited by sexually mature individuals of both *L. fluviatilis* and *L. planeri*. Thus at 9.5°C, oxygen consumption of male and female mature *L. planeri* was 73 and 44 $\mu L \cdot g^{-1} \cdot h^{-1}$, respectively (Lewis and Potter 1977), which are similar to the rates of *L. fluviatilis*. This situation probably reflects the greater activity of

TABLE 3. Changes in oxygen consumption, ventilatory frequency, and heart rate during the life cycle of *L. planeri* and *L. fluviatilis*.

	Mean weight (g)	Months	Temp. (°C)	Oxygen consumption ($\mu L \cdot g^{-1} \cdot h^{-1}$)	Ventilatory frequency (beats min^{-1})	Heart rate (beats min^{-1})
L. planeri[a]						
Larvae	2.81	All	10	20.3	—	—
Stage 6	2.08	Sept.–Feb.	10	50.5	66.2	—
Sexually mature						
males	”	March	10	73.3	110.5	—
females	”	March	10	44.1	71.6	—
Postspawning						
males	”	March–April	10	59.0	85.6	—
females	”	”	10	39.5	61.7	—
L. fluviatilis[a,b]						
Larvae	1.42	All	10	29.3	—	—
Stage 6	1.27	Sept–April	10	60.4	58.5	—
Upstream migrants	46.8	Nov.–Jan.	9.5	26.6	55	24
Prespawning	”	April	9.5	48.2	70	36.5
Sexually mature males	”	May	9.5	63	85	42
Spawning females	”	May	9.5	39	65	38

[a] From Lewis and Potter (1977).
[b] From Claridge and Potter (1975).

the males during spawning (Hardisty and Potter 1971) and the fact that the female increases in weight by taking up a large amount of water at this time (Claridge and Potter 1975).

Hypoxia — The results of Johansen et al. (1973) on the effects of hypoxia on *E. tridentatus* indicated that the adults of this species maintained their oxygen uptake at a constant rate until oxygen concentration fell to 1.33 kPa both at 5 and 10°C, and to 5.33 kPa at 20°C. Below these levels, however, the oxygen-uptake rate tended to fall, particularly at the higher temperature. In contrast to the above pattern of change, the rate of oxygen uptake of *L. fluviatilis* increased progressively with a decline in oxygen, rising from 26.57 $\mu L \cdot g^{-1} \cdot h^{-1}$ at 100% saturation with air to 36.36 $\mu L \cdot g^{-1} \cdot h^{-1}$ at 30% saturation at 9.5°C (Claridge and Potter 1975). Since no increase in activity was observed down to 20% air saturation, this increase is almost certainly due to a rise in the metabolic cost of ventilation, paralleling the situation recorded for trout (Hughes and Saunders 1970). Below 20% saturation with air, however, the animal detached itself from the walls of the chamber and started to swim vigorously, a behavioral trait that presumably parallels the avoidance reaction observed in elasmobranchs and teleosts exposed to potentially lethal low oxygen levels (Randall 1970). Although *L. fluviatilis* is able to survive saturation levels as low as 9.5% of air saturation for at least 96 h, the animals died within 5–8 h at 7.5% air saturation (Claridge and Potter 1975).

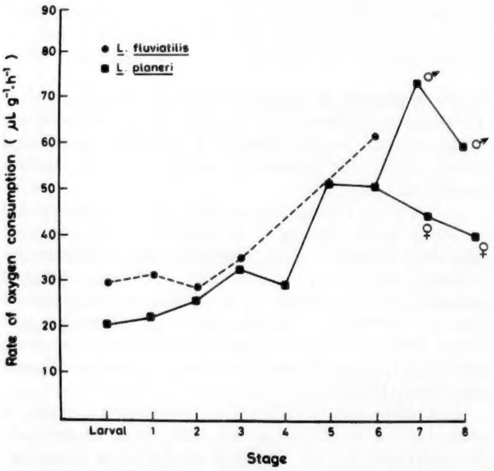

FIG. 5. Mean standard rates of oxygen consumption for larval, metamorphosing (1–6), mature (7), and spent (8) *L. fluviatilis* and *L. planeri* at 9.5°C (after Lewis and Potter 1977).

Swimming — Active oxygen consumption rates have been recorded for both sea lampreys and river lampreys (Table 4). In spite of their poor swimming performance in comparison with teleosts (Beamish 1974), the rates of active oxygen consumption are similar to those of fishes and, in particular, the Salmonidae.

VENTILATION AND HEART RATES

Larvae — Normal, resting, ventilation frequency of

TABLE 4. Comparison of the oxygen uptake of the adults of three species of lampreys.

	Weight (g)	Temp. (°C)	Oxygen uptake ($\mu L \cdot g^{-1} \cdot h^{-1}$)	
P. marinus[a]				
Standard rate	100	5	36.9	Young adults
		10	45.1	
		15	80.0	
		20	86.8	
Standard rate	250–350	5	34.3	
		15	75.7	
		20	81.5	
Active	57.2 (33.6–72.0)	10	332.8	Swimming at 30–40 $cm \cdot s^{-1}$ for 20–60 min
E. tridentatus[b]				
Standard rate	250–300	5	21.2	
		15	34.6	
		20	90.0	
L. fluviatilis[c]				
Standard rate	46.8 (21.4–78.1)	5	10.5	Upstream migrating adults in January
		9.5	26.6	
		16	63.0	
Standard rate	”	5	23.8	Mature adults in March
		9.5	46.9	
		16	107.1	
Active	”	9.5	82.1–409.6	Active, sexually mature

[a] From Beamish (1973).
[b] From Johansen *et al.* (1973).
[c] From Claridge and Potter (1975).

ammocoetes is difficult to measure since, unless provided with a substrate into which the animal can burrow, abnormally high values would be anticipated. However, once the animal has burrowed it is difficult to observe directly. In an experimental regime in which the ammocoetes of *I. hubbsi* were provided with an artificial substrate, some of the animals positioned themselves in such a manner that the ventilatory movements could be observed. At full air saturation at 15°C, frequencies between 72 and 96 beats min^{-1} were obtained (Potter et al. 1970). Frequencies between 30 beats min^{-1} at 4°C and 150 beats min^{-1} at 25°C were recorded for *P. marinus* placed in glass tubes (Rovainen and Schieber 1975) (Table 5).

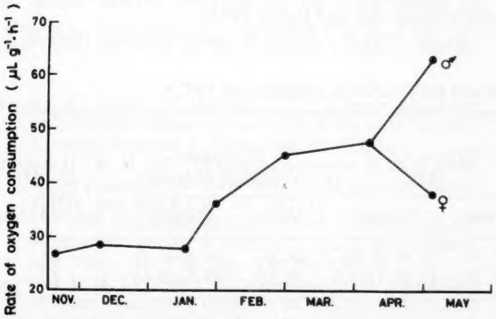

FIG. 6. The mean standard rate of oxygen consumption at 9.5°C for upstream migrating and sexually mature adult *L. fluviatilis* (after Claridge and Potter 1975).

In response to a lowered oxygen tension, ammocoetes of *I. hubbsi* and *P. marinus* increase their ventilation rate (Potter et al. 1970; Rovainen and Scheiber 1975). For example, at an oxygen tension of 1.60–2.13 kPa at 15°C, ammocoetes of *I. hubbsi* maintained an elevated pumping rate of up to 180 beats min^{-1} for as long as 4 d (Potter et al. 1970). At the lower oxygen levels of 0.93–1.33 kPa and 2.67–5.33 kPa, which proved fatal after a few hours, an initial rise in the pumping rate was followed by a decline until death occurred.

As in teleosts, the ventilation volume of ammocoetes increases in response to hypoxia, in *P. marinus* from 1 to 8 $mL \cdot min^{-1}$ (Rovainen and Schieber 1975). At high oxygen tensions the velum is often observed beating without any detectable corresponding movements of the branchial basket, whereas the pharynx exhibits a marked series of contractions during hypoxia.

Adults — In both *L. fluviatilis* and *L. planeri* there is a marked sexual dimorphism and an increase in the

TABLE 5. Comparison of ventilation values for larval *P. marinus* and adult *E. tridentatus*.

	Weight range (g)	Temp. (°C)	Mean resting ventilation volume (mL $min^{-1} \cdot g^{-1}$)	Mean resting frequency (beats min^{-1})	Stroke volume ($\mu L \cdot g^{-1}$)	Oxygen extracted ($mL \cdot L^{-1}$)	% extraction
P. marinus[a] (larvae)	0.44–3.50	20	0.60 (0.3–3.3)	79.2	(4–25)	2.52	43
E. tridentatus[b] (adults)	200–600	14	0.541 (0.253–1.055)	110	4.9 (2.1–9.59)	2.08	19.4 (10–28.4)

[a] From Rovainen and Schieber (1975).
[b] From Johansen et al. (1973).

ventilatory frequency as the animals attain sexual maturity, and a comparable pattern of increase is found in the heart rate of *L. fluviatilis* (Table 3). In the upstream migrating adults, a marked circadian rhythm exists in both the ventilatory and heart rates, the maximum rates being recorded during the night (Claridge et al. 1973), parallelling the time of peak activity in the field at this stage of the life cycle (Hardisty and Potter 1971, Sjöberg 1974, 1977). Both ventilation frequencies and heart rates increase with increasing temperature (Table 2). Although a correlation exists between heart rates and ventilatory frequencies, synchronous coupling between the heart beats and ventilatory pumping was observed in only 2.6% of the recordings obtained from *L. fluviatilis* (Claridge et al. 1973).

Blood oxygenation values have been recorded both at rest and during activity for adults of *E. tridentatus* by Johansen et al. (1973) and summarized in Table 6. During exercise, the percentage of oxygen utilization of the blood more than doubles while the $\dot{Q}/\dot{V}O_2$ value falls, suggesting a compensation by the ventilatory system.

It is extremely difficult to obtain samples of unmixed exhaled water from adult lampreys. By a cannulation technique, however, the ventilation volumes and percentage extraction from the inhalant water have been estimated for adult *E. tridentatus* (Johansen et al. 1973, Table 5). The average values are within the range recorded for teleosts. Of particular interest is the fact that the percentage extraction of oxygen is lower in adults than in ammocoetes of *P. marinus* (19.4% compared with 43%), which suggests that the tidal system of adults is less efficient than the unidirectional system of the larvae (Randall 1972).

When subjected to hypoxia the ventilation frequency and heart rates increase in both *E. tridentatus* and *L. fluviatilis*. In *L. fluviatilis* the ventilation frequency increases from 54.8 beats min^{-1} at 100% saturation to a peak of 140.8 beats min^{-1} at 20% saturation while over the same range the heart rate increased from 23.7 to 26.7 beats min^{-1} (Fig. 7) (Claridge and Potter 1975). In air-saturated water, only the first two pairs of gill pouches were observed pumping, but as the oxygen concentration was lowered, the more posterior pouches started beating, so that by 60% saturation all seven pairs were operating (Claridge and Potter 1975). Thus, the ventilation volume undoubtably rises and the amplitude appears to increase. Below 20% saturation there is a reduction in the ventilation frequency; this apnoea is perhaps a forerunner of total respiratory failure. While the response of the heart to lowered oxygen levels in teleosts and elasmobranchs is bradycardia (Shelton 1970), the heart rate of *L. fluviatilis* increased slightly while the percentage saturation was reduced to 20%, though at lower oxygen levels bradycardia may occur (Claridge and Potter 1975).

As the oxygen content of water declines, there is a

TABLE 6. Blood oxygenation values in inactive and active adult *E. tridentatus* at 10°C.[a]

	Arterial oxygen tension, P_aO_2 (kPa)		Venous oxygen tension, P_vO_2 (kPa)		$P_IO_2 - P_aO_2$[b] (kPa)		% oxygen utilization of blood[c]		$\dot{Q}/\dot{V}O_2$ ratio (mL/mLO_2)
	Mean	(Range)	Mean	(Range)	Mean	(Range)	Mean	(Range)	
Inactive	8.68	(7.73–10.26)	4.47	(3.20–5.60)	6.53	(4.40–8.66)	24.8	(11.4–44.8)	48
Active	6.54	(3.60–9.20)	1.80	(0.99–8.53)	7.70	(5.07–11.53)	58.77	(28.3–85.6)	21

[a] From Johansen et al. (1973).
[b] P_IO_2 is oxygen tension of the inspired water.
[c] This is calculated from $[(S_aO_2 - S_vO_2) \times 100]/S_aO_2$ where S_aO_2 is percentage saturation of the arterial blood and S_vO_2 is percentage saturation of venous blood.

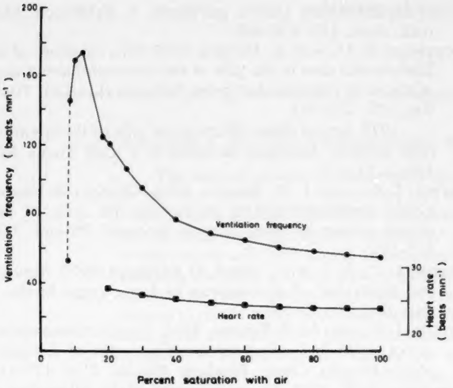

FIG. 7. The ventilation frequency and heart rate of *L. fluviatilis* exposed to a range of saturation with air in January at 9.5°C (from Claridge and Potter 1975).

three- to four-fold increase in the percentage of oxygen utilization of the blood by the tissues, from about 9% at full air saturation to 30% at an oxygen level of 4.00 kPA (Johansen et al. 1973). Arterial saturation remains high as hypoxia progresses and does not drop below 50% until the ambient water has fallen to less than 30% of normal air saturation.

High oxygen affinity, oxygen capacity, and the large Bohr effect of the blood of *E. tridentatus* (Johansen et al. 1973) are all conducive to withstanding low ambient oxygen levels while, in addition, the high venous oxygen saturation at rest in normoxic water probably provides an important oxygen reserve. This high oxygen affinity develops during metamorphosis when there is a complete change in the hemoglobins (Potter and Brown 1975) resulting in a pronounced shift in the oxygen affinity of the blood (Bird et al. 1976).

These changes are almost certainly related to the far greater activity exhibited by the adult during its predatory, migratory, and spawning phases, compared with those exhibited by the relatively sedentary larvae.

BARNES, K., AND M. W. HARDISTY. 1972. Ultrastructural and histochemical studies on the testis of the river lamprey, *Lampetra fluviatilis*. J. Endocrinol. 53: 59–69.

BEAMISH, F. W. H. 1973. Oxygen consumption of adult *Petromyzon marinus* in relation to body weight and temperature. J. Fish. Res. Board Can. 30: 1367–70.

1974. Swimming performance of adult sea lamprey, *Petromyzon marinus*, in relation to weight and temperature. Trans. Am. Fish. Soc. 103: 355–358.

BEAMISH, F. W. H., AND P. S. MOOKHERJII. 1964. Respiration of fishes with special emphasis on standard oxygen consumption. 1. Influence of weight and temperature on respiration of goldfish, *Carassius auratus*, L. Can. J. Zool. 42: 161–175.

BIRD, D. J., P. L. LUTZ, AND I. C. POTTER. 1976. Oxygen dissociation curves of the blood of larval and adult lampreys, (*Lampetra fluviatilis*). J. Exp. Biol. 65: 449–458.

BOURQUE, S. 1970. Temperature effects on oxygen consumption and blood properties in the artic lamprey, *Lampetra japonica*. M.Sc. thesis, Univ. Alberta, Edmonton, Alta.

BRETT, J. R. 1973. Energy expenditure of Sockeye salmon, *Oncorhynchus nerka*, during sustained performance. J. Fish. Res. Board Can. 30: 1799–1809.

BYCZKOWSKA-SMYK, W. 1958. The respiratory surface of the gills in Teleosts. II. The respiratory surface of the gills in the eel (*Anguilla anguilla* L.) the loach (*Misgurnus fossilis* L.) and the perch-pike (*Lucioperca lucioperca* L.) Acta Biol. Cracov. 1: 83–97.

CLARIDGE, P. N., AND I. C. POTTER. 1975. Oxygen consumption, ventilatory frequency and heart rate of lampreys (*Lampetra fluviatilis*) during their spawning run. J. Exp. Biol. 63: 193–206.

CLARIDGE, P. N., I. C. POTTER, AND G. M. HUGHES. 1973. Circadian rhythms of activity, ventilatory frequency and heart rate in the adult river lamprey, *Lampetra fluviatilis*. J. Zool. (Lond.) 171: 239–250.

CREASER, C. W., AND C. S. HANN. 1929. The food of larval lampreys. Pap. Mich. Acad. Sci. 10: 433–437.

CZOPEK, J. C. 1970. Survival ability in the river lamprey under conditions of partial or complete elimination of gill respiration. Bull. Acad. Pol. Sci. (Sci. Biol.) 18: 237–240.

CZOPEK, J. C., AND O. SAWA. 1971. The structure and vascularization of the skin and of the gills in the river lamprey (*Lampetra fluviatilis* L.) Acta Anat. 79: 305–320.

DAMAS, H. 1935. Contribution à l'étude de la métamorphose de la tête de la lamproie. Arch. Biol. Paris 46: 171–227.

DAWSON, J. 1905. The breathing and feeding mechanisms of the lampreys. Biol. Bull. Mar. Biol. Lab. (Woods Hole, Mass.) 9: 1–21, 91–111.

DOWNING, S. W., AND R. R. NOVALES, 1971. The fine structure of lamprey epidermis. 1. Introduction and mucous cells. J. Ultrastruct. Res. 35: 282–294.

FARMER, G. J., AND F. W. H. BEAMISH. 1969. Oxygen consumption of *Tilapia nilotica* in relation to swimming speed and salinity. J. Fish. Res. Board Can. 26: 2807–2821.

HARDISTY, M. W., AND I. C. POTTER. 1971. The general biology of adult lampreys, p. 127–206. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London.

HILL, B. J., AND I. C. POTTER. 1970. Oxygen consumption in ammocoetes of the lamprey *Ichthyomyzon hubbsi* Raney. J. Exp. Biol. 53: 47–57.

HILLS, B. A., AND G. M. HUGHES. 1970. A dimensional analysis of oxygen transfer in the fish gill. Resp. Physiol. 9: 126–140.

HUGHES, G. M. 1966. The dimensions of fish gills in relation to their function. J. Exp. Biol. 45: 177–195.

1970. Morphological measurements of the gills of fishes in relation to their respiratory function. Folia Morphol. Praha 18: 78–95.

1972. Morphometrics of fish gills. Resp. Phys. 14: 1–25.

1977. Dimensions and the respiration of lower vertebrates, p. 57–81. *In* T. J. Pedley [ed.] Scale effects in animal locomotion. Academic Press, London.

1978. Some features of gas transfer in fish. Bull. Inst. Math. 14: 39–43.

1979. Scanning electron microscopy of the respiratory surfaces of trout gills. J. Zool., (Lond.) 188: 443–453.

HUGHES, G. M., AND I. E. GRAY. 1972. Dimensions and ultrastructure of toadfish gills. Biol. Bull. 143: 150–161.

HUGHES, G. M., AND M. MORGAN. 1973. The structure of fish gills in relation to their respiratory function. Biol. Rev. 48: 419–475.

HUGHES, G. M., AND R. L. SAUNDERS. 1970. Responses of the respiratory pumps to hypoxia in the rainbow trout (*Salmo gairdneri*). J. Exp. Biol. 53: 529–545.

HUGHES, G. M., AND D. E. WRIGHT. 1970. A comparative study of the ultrastructure of the water-blood pathway in the secondary lamellae of Teleost and Elasmobranch fishes — benthic forms. Z. Zellforsch. Mikrosk. Anat. 104: 478–493.

JARVIK, E. 1964. Specializations in early vertebrates. Annl. Soc. R. Zool. Belg. 94: 11–95.

1968. Aspects of vertebrate phylogeny, p. 497–527. *In* T. Ørvig [ed.] Current problems of lower vertebrate phylogeny. Interscience London, Sydney.

JOHANSEN, K., C. LENFANT, AND D. HANSON. 1973. Gas exchange in the lamprey, *Entosphenus tridentatus*. Comp. Biochem. Physiol. 44A: 107–119.

KOROLEWA, N. W. 1964. Water respiration of lamprey and its survival in a moist atmosphere. Izv. Vses. Nauchno-Issled. Inst. Ozern. Rechn. Rybn. Khoz. 58: 186–190. (In Russian).

LEACH, W. J. 1946. Oxygen consumption of lampreys, with special reference to metamorphosis and phylogenetic position. Physiol. Zool. 19: 365–374.

LEWIS, S. V. 1976. Respiration and gill morphology of the paired species of lampreys. *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). Ph.D. thesis, Univ. Bath, England.

LEWIS, S. V., AND I. C. POTTER. 1976a. Gill morphometrics of the lampreys *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). Acta Zool. Stockh. 57: 103–112.

1976b. A scanning electron microscope study of the gills of the lamprey, *Lampetra fluviatilis* (L.) Micron 7: 205–211.

1977. Oxygen consumption during the metamorphosis of the parasitic lamprey, *Lampetra fluviatilis* (L.) and its non-parasitic derivative, *Lampetra planeri* (Bloch). J. Exp. Biol. 69: 187–198.

MOORE, J. W., AND I. C. POTTER. 1976. Aspects of feeding and lipid deposition and utilization in the lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). J. Anim. Ecol. 45: 699–712.

MORGAN, M. 1974. Development of the secondary lamellae of the gills of the trout, *Salmo gairdneri* (Richardson). Cell Tissue Res. 151: 509–523.

MORRIS, R., AND A. D. PICKERING. 1975. Ultrastructure of the presumed ion-transporting cells in the gills of ammocoete lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). Cell Tissue Res. 163: 327–341.

1976. Changes in the ultrastructure of the gills of the river lamprey, *Lampetra fluviatilis* (L.), during the anadromous spawning migration. Cell Tissue Res. 173: 271–277.

MOY-THOMAS, J. A. 1971. Palaeozoic fishes. Chapman and Hall, London.

MUIR, B. S., AND G. M. HUGHES. 1969. Gill dimensions of three species of tuna. J. Exp. Biol. 51: 271–285.

NAKAO, T. 1974. Fine structure of the agranular cytoplasmic tubules in the lamprey chloride cells. Anat. Rec. 178: 49–61.

NAKAO, T., AND K. UCHINOMIYA. 1974. Intracisternal tubules of lamprey chloride cells. J. Electron Microsc. 23: 51–55.

OLSON, K. R., AND P. O. FROMM. 1973. A scanning electron microscopic study of secondary lamellae and chloride cells of rainbow trout (*Salmo gairdneri*). Z. Zellforsch. Mikrosk. Anat. 143: 439–449.

PICKERING, A. D., AND R. MORRIS. 1976. Fine structure of the interplatelet area in the gills of the macrophthalmia stage of the river lamprey, *Lampetra fluviatilis* (L.). Cell Tissue Res. 168: 433–443.

1977. Sexual dimorphism in the gills of the spawning river lamprey, *Lampetra fluviatilis* (L.). Cell Tissue Res. 180: 1–10.

POTTER, I. C., AND I. D. BROWN. 1975. Changes in haemoglobin electropherograms during the life cycle of two closely related lampreys. Comp. Biochem. Physiol. 51B: 517–519.

POTTER, I. C., B. J. HILL, AND S. GENTLEMAN. 1970. Survival and behaviour of ammocoetes at low oxygen levels. J. Exp. Biol. 53: 59–73.

POTTER, I. C., AND M. J. ROGERS. 1972. Oxygen consumption in borrowed and unburrowed ammocoetes of *Lampetra planeri* (Bloch). Comp. Biochem. Physiol. 41A: 427–432.

RAJBANSHI, V. K. 1977. The architecture of the gill surface of the catfish, *Heteropneustes fossilis* (Bloch): SEM study. J. Fish Biol. 10: 325–329.

RANDALL, D. J. 1970. Gas exchange in fish, p. 253–291. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. 4. Academic Press, London.

1972. Respiration, p. 287–306. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2. Academic Press, London.

ROBERTS, T. D. M. 1950. The respiratory movements of the lamprey (*Lampetra fluviatilis*). Proc. R. Soc. Edinburgh Sect. B, 64: 235–252.

ROGERS, M. J. 1971. Oxygen consumption in burrowed and unburrowed ammocoetes of *Lampetra planeri* (Bloch). B.Sc. project report, Univ. Bath, England.

ROVAINEN, C. M., AND M. H. SCHIEBER. 1975. Ventilation of larval lampreys. J. Comp. Physiol. 104: 185–203.

SCHROLL, F. 1959. Zur Ernährungsbioloe der steirischen Ammocöten *Lampetra planeri* (Bloch) und *Eudontomyzon danfordi* (Regan). Int. Rev. Gesamten Hydrobiol. Hydrogr. 44: 395–429.

SHELTON, G. 1970. The regulation of breathing, p. 293–359. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. 4. Academic Press, London.

SJÖBERG, K. 1974. Spawning period, locomotor activity and length/weight of the river lamprey, (*Lampetra fluviatilis* (L.)) in the Rickleå River, province of Västerbotten, Sweden. Zool. Revy 36: 41–48.

1977. Locomotor activity of river lamprey *Lampetra fluviatilus* (L.) during the spawning season. Hydrobiologia 55: 265–270.

STAHL, B. J. 1974. Vertebrate history: Problems in evolution. McGraw-Hill, Inc., NY.

STENSIÖ, E. 1968. The cyclostomes with special references to the diphyletic origin of the Petromyzontida and Myxinoidea, p. 13–71. *In* T. Ørvig [ed.] Current problems of lower vetebrate phylogeny. Interscience, London, Sydney.

STERBA, G. 1953. Die Physiologie und Histogenese der Schildrüse und des Thymus beim Bachneunauge (*Lampetra planeri* Bloch = *Petromyzon planeri* Bloch) als Grundlogen phylogenetischer Studien über die Evolution der innersekre-torischen Kiemendarmderivake. Wiss. Z. Friedrich-Schiller-Univ. Jena Math.-Naturwiss. Réihe 2: 239–298.

YOUSON, J. H., AND P. A. FREEMAN. 1976. Morphology of the gills of larval and parasitic adult sea lampreys. J. Morphol. 149: 73–104.

Neurophysiology of Lampreys[1]

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ROVAINEN, C. M. 1980. Neurophysiology of lampreys. Can. J. Fish. Aquat. Sci. 37: 1723–1738.

The nervous system of the lamprey has been appreciated by comparative neuroanatomists for nearly a century as a "prototype" for the brain and spinal cord of higher vertebrates. Only recently have neurophysiologists discovered the practical advantages of the lamprey brain and spinal cord, such as relative simplicity, survival in isolation, and the occurrence of large, visible, nerve cells and axons. During the past 15 yr rapid progress has been made in understanding the basic physiological, pharmacological, and ultrastructural properties of lamprey neurons and the organization of sensory and motor systems. Several types of neurons are now known in considerable detail and include the prominent Müller and Mauthner cells, respiratory and spinal motoneurons, giant interneurons, and sensory dorsal cells. Some of the important subjects for future research include the behavioral responses of adult lampreys to different modes of sensory stimulation, the neural control of feeding, and the changes which occur in the nervous system during metamorphosis.

Key words: brain, lamprey, neurophysiology, respiration, spinal cord, swimming

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Depuis presque un siècle, les spécialistes de l'anatomie comparée considèrent le système nerveux de la lamproie comme «prototype» du cerveau et de la moelle épinière des vertébrés supérieurs. Ce n'est que récemment que les neurophysiologistes découvrirent les avantages pratiques du cerveau et de la moelle épinière : simplicité relative, survie une fois isolés et présence de cellules nerveuses et d'axones gros et visibles. On a fait beaucoup de progrès ces 15 dernières années et l'on comprend mieux les propriétés physiologiques, pharmacologiques et microscopiques fondamentales des neurones de lamproie, ainsi que l'organisation des appareils sensoriel et moteur. On connaît maintenant dans leurs détails plusieurs types de neurones, y compris les proéminentes cellules de Müller et Mauthner, les motoneurones respiratoires et spinaux, les interneurones géants et les cellules dorsales sensorielles. Parmi les importants sujets de recherche future, on note le comportement de lamproies adultes en réponse à différents stimuli sensoriels, le contrôle neural de l'alimentation et les changements qui se produisent dans le système nerveux durant la métamorphose.

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Two general goals in neurophysiology are the description of the fundamental properties of neurons and the explanation of behavior in terms of activities in neural circuits. The lamprey is an excellent subject for both types of studies. First, the brain and spinal cord can be removed from the lamprey and can survive for many hours or days in isolation. Second, the spinal cord and the walls of the brain are relatively transparent, and multiple intracellular electrodes can be placed in visible nerve cells and axons. Third, the lamprey brain stem and spinal cord are relatively simple. Some large cells such as the Müller and Mauthner neurons can be recognized individually in different animals. These cells have stereotyped synaptic connections with other neurons, and intracellular stimulation of their axons can elicit simple behavioral responses in adult lampreys and in ammocoetes. Thus, the functions of single neurons can be determined more easily in the lamprey than in more complicated animals. Finally, the nervous system of the lamprey has an anatomical and physiological organization similar to that of higher vertebrates. Although many invertebrate ganglia are also simple and convenient for electrical recording, their neurons exhibit many unusual cellular and organizational properties that limit their usefulness as models for vertebrate neurons. Thus, the lamprey, despite its unpleasant appearance and destructive feeding habits, attractively combines in its nervous system a number of experimental advantages and relevance to higher vertebrates.

The nervous system of the lamprey has been described extensively in the classical and modern literature. Topics which have been reviewed recently include the nervous system in general (Healey 1972; Rovainen 1979b), neuroanatomy (Nieuwenhuys 1977),

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Müller and Mauthner cells (Rovainen 1978), neural control of respiration (Rovainen 1977), sense organs (Kleerekoper 1972), and brain–pituitary relation (Gorbman 1980). This review will concentrate upon the properties of lamprey neurons and their physiological organization in motor systems for swimming and for breathing. Since comprehensive literature citations are available elsewhere (Healey 1972; Kleerekoper 1972; Rovainen 1979b), recent contributions and important classical papers on the lamprey nervous system will be emphasized here.

Basic Organization and Properties of the Lamprey Nervous System

NEUROANATOMY

The brain of the lamprey has always attracted the attention of comparative neuroanatomists as a result of the special phylogenetic position of this animal. The structure of the brain appears to be similar among various species of lampreys, although a thorough survey for possible differences has not been attempted. Descriptions of groups of nerve cells and tracts in the brain of *Lampetra (planeri?)* ammocoetes by Tretjakoff (1909b) and in adult *L. lamottenii* by Johnston (1902) appear to be generally applicable to other species. The brain of adult *L. fluviatilis* is the one most recently and thoroughly described (Heier 1948; Schober 1964; Schwab 1973; Petrovický 1977; Nieuwenhuys 1977). Other papers have described the brains of *L. japonica* (Saito 1930), *L. planeri* (Stefanelli 1934; Schober 1964), *Petromyzon marinus* (Ahlborn 1883; Stefanelli 1934, 1937; Larsell 1947; Kennedy and Rubinson 1977; Rubinson and Kennedy 1980), *Ichthyomyzon* spp. (Johnston 1912; Herrick and Obenchain 1913; Woodburne 1936; Larsell 1947; Northcutt 1979a, b), and *Entosphenus tridentatus* (Larsell 1947). Older anatomical tracings of tracts in the lamprey brain relied on the histology of normal animals, and only recently have the more accurate degeneration and peroxidase transport methods been used (Kennedy and Rubinson 1977; Kosareva et al. 1977; Homma 1978; Finger and Rovainen 1978; Northcutt 1979a, b). Electron-microscopic studies have shown that nerve terminals in the brain of *P. marinus* adults and ammocoetes have the typical structure of chemical synapses (Wickelgren 1977a; Christensen and Quinn 1979). Most of the terminals contain round synaptic vesicles and are presumably excitatory, and others contain flattened vesicles and may be inhibitory. Synapses on proximal and on distal dendrites of Müller cells do not differ statistically with respect to numbers of vesicles or lengths of specialized membranes (Christensen and Quinn 1979). Some terminals in the brain of *L. planeri* also contain large, dense-cored vesicles, which resemble those in peptide-secreting neurons (Sterba et al. 1979).

The spinal cord of adult lampreys and of large ammocoetes is flat, with nerve cells situated in a horizontal sheet which is surrounded by tracts of longitudinal axons. Because of its lack of myelin, the living cord is transparent, and various giant axons and nerve cells are usually visible. The structure and function of the various types of sensory cells, motoneurons, and interneurons which have been identified in the spinal cord of lampreys, especially of *P. marinus*, have been reviewed in detail (Rovainen 1979b). These and additional types of interneurons have recently been described histologically in adult *Ichthyomyzon unicuspis* and in ammocoetes of *P. marinus* in Nissl-stained whole mounts (Selzer 1979a) and after retrograde labeling with peroxidase (Tang and Selzer 1979). The ultrastructure of the spinal cord has been described in *Lampetra* spp. (Bertolini 1964) and in *P. marinus* (Schultz et al. 1956; Smith et al. 1970; Smith 1971; Pfenninger and Rovainen 1974). Nakao (1979) has described the ultrastructure of the meningeal tissue around the spinal cord in adult *L. japonica* and has revised the classical accounts of the meninges based on light microscopy (Sterzi 1907; Ariëns Kappers 1926).

SENSORY SYSTEMS

The structure and function of the specialized sensory systems in the lamprey have been excellently reviewed by Kleerekoper (1972). His description of the olfactory system was particularly thorough. Important recent work on this system has been a behavioral survey for pheromones by Teeter (1980) and his colleagues and intracellular recording from olfactory receptors by Suzuki (1974). Olfactory sensory cells have the typical electrical properties of neurons, and applications of L-arginine produce depolarizations accompanied by increases in cellular conductance. In later extracellular recordings of the firing of the sensory cells, Suzuki (1978) demonstrated that excitation of the receptors by arginine requires Ca^{++} in the fluid bathing the olfactory sac. The central projections of the olfactory nerve into the lamprey brain are well known (Nieuwenhuys 1967), and electrical stimulation of the olfactory nerve in *L. fluviatilis* produces typical extracellular potentials in the olfactory bulb and other parts of the telencephalon (Bruckmoser 1971).

The general structure of the lateral eyes in adult lampreys has been well reviewed (Walls 1963; Kleerekoper 1972). The most important recent work on the eye has concerned the ultrastructure of the retina in adult *L. fluviatilis*, including the photoreceptors (Öhman 1971, 1976), pigment epithelium (Ohman 1974), inner synaptic layer (Holmberg 1978a), and axons in the retina (Holmberg 1978b) and in the optic nerve (Öhman 1977). Catecholamines have been demonstrated in some of the amacrine cells in the retina (Ehinger et al. 1977). The ultrastructure of the retina in ammocoetes (Dickson and Collard 1979) and adult *P. marinus* (Dickson and Graves 1979) has also been described. The anatomical projections of the optic nerve into the brains of *P. marinus* ammocoetes and adults have been determined with degeneration staining (Kennedy and Rubinson 1977) and in adult *L. fluviatilis* by peroxidase transport (Kosareva et al. 1977). Electrical recordings have been made from the retina of adult *L. fluviatilis* (Holmberg et al. 1977; Dreyfert et al. 1979) and of *P. marinus* (Rubinson et al. 1977) during light flashes. Responses to photic stimuli to the eyes have also been recorded in the optic tectum (Veselkin 1966) and in reticulospinal cells (Wickelgren 1977a).

The pineal of the lamprey is a luminosity detector (review: Eddy 1972). The ultrastructure on the pineal photoreceptors in *Lampetra* is well known (Bertolini and Mangia 1966; Collin 1968, 1969; Collin and Meiniel 1968a, b). Intracellular recordings from the pineal of *P. marinus* ammocoetes have demonstrated that the photoreceptors exhibit graded hyperpolarizations to light flashes (Pu and Dowling 1980).

The structure of the vestibular labyrinths has been determined with light and electron microscopy for adult *L. fluviatilis* (Lowenstein et al. 1968) and for a series of embryos and small ammocoetes of the same species (Thornhill 1972). The ultrastructure of the macular hair cells of adult *L. japonica* has also been described with scanning and transmission electron microscopy (Hoshino 1975). The projections of vestibular afferents in the medulla have been reinvestigated with modern degeneration staining in *P. marinus* ammocoetes (Rubinson 1974) and in adult *I. unicuspis* (Northcutt 1979b). The ultrastructure of mixed electrotonic and chemical synapses from vestibular afferent axons to large neurons in the vestibular nuclei of *L. planeri* has been described by Stefanelli and Caravita (1970). The physiology of the lamprey vestibular system is reviewed in a later section.

Johnston (1905), Tretjakoff (1927a), and Lindström (1949) have provided good anatomical descriptions of the peripheral projections of the trigeminal and other cranial nerves in *Lampetra* ammocoetes and adults. Northcutt (1979a) has determined the central projections of the trigeminal nerve in *I. unicuspis* with degeneration staining. Trigeminal ganglion cells in adult *P. marinus* respond to mechanical stimulation of the skin of the sucker and head and can be classified as touch, pressure, and pain receptors (Matthews and Wickelgren 1978a). The ultrastructure of neuromast organs on the head of *L. japonica* has been described by Yamada (1973). Sensory neurons from neuromasts on the head of *P. marinus* respond well to touch stimuli (Matthews and Wickelgren 1978a), but their sensitivity to fluid movement has not yet been demonstrated.

GENERAL NEUROPHYSIOLOGY

The electrical properties of large unmyelinated axons and of their synapses on motoneurons and interneurons have been well studied in the isolated spinal cord of recently metamorphosed *P. marinus*. Some of these findings have been confirmed in ammocoetes and in adult lampreys of other species. Action potentials in Müller axons and in dorsal cells apparently are produced by the usual permeability changes for Na^+ and K^+ and are blocked by tetrodotoxin (Martin and Ringham 1975; Selzer 1979b). External Ca^{++} is not required for action potentials but has marked effects on threshold for firing (Matthews and Wickelgren 1977). Conduction velocities of the largest axons in the spinal cord are as high as $7\ m \cdot s^{-1}$ (Batueva and Shapovalov 1977), and smaller axons conduct action potentials at velocities which are approximately proportional to the square root of their diameters (E. S. Cosbey and C. Rovainen unpublished data).

The most common type of excitatory synapse between large axons and nerve cells in the lamprey uses combined electrotonic and chemical transmission. As observed with electron microscopy, synaptic vesicles cluster against the borders of Müller axons and form typical chemical synaptic junctions on dendritic processes of nerve cells (Bertolini 1963; Smith et al. 1970). Gap junctions, the morphological correlates of electrotonic synapses, often appear near the chemical junctions to form morphologically mixed synapses (Rovainen 1974a, b; Pfenninger and Rovainen 1974; Matthews and Wickelgren 1978b). Christensen (1976) has reconstructed all of the gap and chemical junctions of one combined synapse on a giant interneuron. In physiological experiments, intracellular stimulation of single presynaptic axons elicits synaptic potentials with two components in postsynaptic cells. The initial electrotonic component occurs at short latency, is constant during repetitive stimulation, and is unaffected by removal of external Ca^{++}. The second component, which is produced by chemical transmission, occurs after an additional delay, can increase or decrease in amplitude during repetitive stimulation, and is eliminated reversibly in Ca^{++}-free fluid (Rovainen 1974a, b; Batueva and Shapovalov 1977; Shapovalov 1977; Selzer 1978b). Electrotonic coupling (Ringham 1975) and the voltage dependence of transmitter release (Martin and Ringham 1975) have been studied in detail at the synapses of bulbar Müller axons onto lateral interneurons. The electrotonic synaptic potential in giant interneurons has also been used to confirm and elaborate a general electrical model for vertebrate nerve cells (Christensen and Teubl 1979a, b). Unusual subthreshold depolarizations and hyperpolarizations observed in Müller axons during activity in the spinal cord are probably produced by the backwards spread of action and synaptic potentials from nerve cells through electrotonic synapses into the presynaptic axons (Matthews and Wickelgren 1978b, c; Tamarova 1978).

The isolated spinal cord and brain of the lamprey are very convenient for testing the effects of drugs and putative transmitters on neurons of the central nervous system. Two possible inhibitory transmitters, glycine and γ-aminobutyric acid (GABA), have been applied to giant interneurons in the spinal cord of adult *P. marinus* and *I. unicuspis* (Homma and Rovainen 1978) and to Müller cells in the brain of *P. marinus* (Matthews and Wickelgren 1979a) and of *L. planeri* and *L. fluviatilis ammocoetes* (Martin 1978). These studies demonstrate that glycine and GABA produce increases in Cl^- permeability in nerve cells of the lamprey, and that their effects are antagonized in different ways by the convulsant drugs strychnine, picrotoxin, and bicuculline. Taurine and β-alanine produce inhibitory effects similar to those of glycine on giant interneurons (Homma 1979). Glutamate excites giant interneurons (Martin et al. 1970) and Müller cells by increasing permeabilities to Na^+ and probably to K^+ (Matthews and Wickelgren 1979b). Glutamate and other acidic amino acids excite spinal interneurons and produce swimming activities in *I. unicuspis* (Poon 1980). Müller axons in the spinal cord do not appear to respond directly to amino acids, but they are depolarized by bath applications of glutamate and are hyperpolarized by glycine and GABA, probably through their electrotonic coupling with sensitive nerve cells (Matthews and Wickelgren 1979a, b). Dopamine, noradrenalin, and serotonin are present in small fluorescent nerve cells and fibers in the hypothalamus, brain stem, and ventral spinal cord of *L. fluviatilis* (Baumgarten 1972; Konstantinova 1973), *L. japonica* (Honma 1969, 1970; Ochi and Hosoya 1974), and *P. marinus* (C. Rovainen unpublished data). However, these amines do not produce obvious responses when applied to the spinal cord (Poon 1980) or to Müller cells (Matthews and Wickelgren 1979a). Acetylcholine is the probable transmitter released by lamprey motoneurons, but otherwise does not appear to be a major transmitter in the brain stem or spinal cord. Giant interneurons (Martin et al. 1970) and Müller cells (Matthews and Wickelgren 1979a) do not respond to acetylcholine. Likewise, transmission through various sensory and spinal systems continues in the presence of curare (Wickelgren 1977a; Rovainen 1978). Other regions of the brain of adult *L. fluviatilis* with possible cholinergic transmission based on cholinesterase staining have been described by Wächtler (1974). Both acetylcholinesterase and cholinacetyl transferase activities have been measured chemically in the lamprey brain and are lower than in most other vertebrates (Wächtler 1978). The lamprey spinal cord is a good preparation for general neuropharmacological studies. The anticonvulsant phenytoin suppresses chemical synaptic potentials (Selzer 1978b) and weakens the action potentials in dorsal cells (Selzer 1979b). Guanidine reduces the threshold for firing in Müller axons (Matthews and Wickelgren 1977). Opiate receptors have been reported in the brain of adult *L. fluviatilis*, but benzodiazepine binding was not detected (Fernholm et al. 1979). Most of the drugs with important effects on the nervous system have not yet been tested in the lamprey.

METABOLISM OF LAMPREY BRAIN AND MENINGES

The lamprey brain, like nervous tissue of higher vertebrates, utilizes glucose and stored glycogen as the main substrates for energy. The rates of glycolysis in brains of *P. marinus* ammocoetes at 20–26°C were 0.2–0.4 μmol glycosyl units $\cdot g^{-1}$ wet wt $\cdot min^{-1}$ (Rovainen et al. 1969). The metabolic rate of isolated brains of adult *L. fluviatilis* in terms of oxygen consumption was 0.7 $\mu mol\ O_2 \cdot g^{-1} \cdot min^{-1}$ (Plisetskaya 1967), a rate many times higher than that for the whole animal on the basis of weight (Claridge and Potter 1975; Lewis and Potter 1977). Among vertebrate nervous tissues, the lamprey brain has one of the highest concentrations of glycogen (Plisetskaya 1967, 1968) and of phosphocreatine (Rovainen et al. 1969).

The meningeal tissues around the brain and above the spinal cord of *P. marinus* and other species of lampreys contain considerable glycogen and produce glucose during metabolic stress (Rovainen 1970; Rovainen et al. 1971). Glucose-6-phosphatase is present in the meningeal tissue (Rovainen 1970; Rovainen et al. 1971; Ogorodnikova and Fomina 1977) and can mediate the final reaction during glucose production from glycogen. The hypothesis that glucose from the meninges could enter the brain was supported by observations of diffusion pathways between the two tissues with electron microscopy, of increases in glucose concentrations in brain tissue during glucose production in meninges, and of penetration of dyes from the meninges into the brain (Rovainen et al. 1971). Unusual round cells in lamprey meningeal tissues are the sites of glycogen storage (Gage 1917; Tretjakoff 1927b) and probably of glucose production. Ultrastructurally, the round cells contain dense deposits of glycogen particles, extensive layers of smooth endoplasmic reticulum, mitochondria, lipid droplets, membrane-bound granules, and vesicles at the surface membrane (Müller 1968; Rovainen et al. 1971).

Under normal conditions glucose and oxygen are probably supplied to the brain and spinal cord by the circulatory system. Blood vessels form a rich network over the surface of the lamprey spinal cord without penetrating it (Sterzi 1907). The ammocoete brain also has a rich supply of blood vessels at its external boundary with meningeal tissue (Hibbard 1963b). In adult lampreys and in ammocoetes of some species, looplike capillaries extend into the brain itself (Sterzi 1907; Rovainen et al. 1971). Circulation to the lamprey brain has not been studied physiologically.

CHANGES IN THE NERVOUS SYSTEM DURING METAMORPHOSIS AND AFTER INJURY

The external transformation of the ammocoete to the macrophthalmic lamprey is accompanied by growth, development, and reorganization of the nervous system. The changes which occur in the brain and spinal cord probably take place without proliferation of additional nerve cells, as indicated by the lack of cell divisions in the ependyma of large ammocoetes of *L. planeri* (Pfister 1971a, b) prior to metamorphosis. However, cells in the olfactory epithelium proliferate during metamorphosis (Leach 1951) and continue to incorporate [^{3}H]thymidine in adults (Thornhill 1970). Most nerve cells and axons in the lamprey brain and spinal cord increase in size during metamorphosis. The physiological properties and functions of some of these neurons, for instance, the Müller and Mauthner cells, V cells, spinal motoneurons, dorsal cells, and giant interneurons, are similar in ammocoetes and in adult lampreys (Rovainen 1967a, 1979a, b).

The visual system matures and becomes functional during transformation of the lamprey. The small lateral eyes of ammocoetes form during embryonic stages (Damas 1944) and grow slowly during larval life (Kiebel 1927). Nerve fibers are present in the optic nerve and project to the contralateral tectum in *P. marinus* ammocoetes (Kennedy and Rubinson 1977). Some proliferation of cells in the optic tectum probably continues in *L. planeri* ammocoetes up to 9 cm in length (Pfister 1971b). The eye of *P. marinus* ammocoetes is undifferentiated except near the optic nerve (Dickson and Collard 1979) and lacks measurable photopigment and electrical responses to light (Rubinson et al. 1977). Stimulation of the optic nerve in ammocoetes does not yet elicit synaptic potentials in Müller cells (Rovainen 1967a). Growth of the eye accelerates prior to metamorphosis, and by stage IV of transformation in *P. marinus* (Manion and Stauffer 1970) the cornea has cleared, photopigment can be measured in the retina, and light flashes can elicit electrical activity (Rubinson et al. 1977). A new ipsilateral visual projection appears in the lamprey brain after metamorphosis (Kennedy and Rubinson 1977), and the nerve cells in the optic tectum grow in size and complexity (Rubinson and Kennedy 1979).

The trigeminal system of lampreys changes dramatically during transformation. Histological observations indicate that nearly all the head muscles innervated by the trigeminal nerve in ammocoetes degenerate and are replaced by new muscles of the sucker and piston in adult *L. fluviatilis* and *L. planeri* (Damas 1935) and *Eudontomyzon mariae* (Balabai 1946). Trigeminal motoneurons to head muscles of ammocoetes and adults have been identified physiologically and anatomically in *L. lamottenii*, *L. aepyptera*, and *I. unicuspis* (Homma 1978). The positions of groups of motoneurons in relation to peripheral muscles are similar for both stages. The hypothesis was proposed that trigeminal motoneurons are retained during metamorphosis and shift their synaptic connections from larval to adult muscles, although degeneration of some neurons and growth of axons from immature nerve cells were not ruled out (Homma 1978). Other motoneurons, such as those to the extraocular muscles and to the dorsal fins, grow and probably mature physiologically during metamorphosis.

The spinal cord of ammocoetes is capable of regeneration after injury in *L. fluviatilis* (Marón 1959) and *P. marinus* (Hibbard 1963a; Niazi 1963; Rovainen 1976a; Selzer 1978a; Wood and Cohen 1979). Following transection of the cord, ependymal tissue grows into the wound from the central canal and forms a pathway for regenerating axons (Marón 1959). Müller and Mauthner axons (Rovainen 1976a; Wood and Cohen 1979) and axons of giant interneurons and dorsal cells (Selzer 1978a) do not grow more than a few millimetres beyond the lesion. Regenerated axons also lie in abnormal positions and are branched (Rovainen 1976a; Wood and Cohen 1979), although they form typical chemical synapses ultrastructurally (Wood and Cohen 1979). Despite the incomplete and abnormal regeneration of large axons, the behavior of small ammocoetes following spinal regeneration is indistinguishable from normal animals (Rovainen 1976a).

Neurophysiology of Swimming

One of the most important activities of adult lampreys is swimming, whether for migration, escape, or attack. Lampreys are effective swimmers over short distances, although their sustained performance is not as good as that of some teleosts (Beamish 1974). The neurophysiology of swimming in higher fish has been reviewed (Grillner and Kashin 1976) and appears to be similar in lampreys. Both ammocoetes and adult lampreys swim by lateral body undulations produced by patterned contractions in the myotomal muscles. These regions of contractions alternate on the two sides of the body and sweep caudally. The wavelength of undulation is approximately equal to the length of the lamprey, and an S-shaped posture of the body is produced in alternate directions (Poon 1980; C. Rovainen unpublished data). The initial burrowing behavior of ammocoetes consists of intensified swimming movements, but in a second phase the movements of the tail are suppressed while the rostral parts of the body crawl through the substrate (Sawyer 1959). In contrast to swimming, crawling behavior in ammocoetes and adult lampreys is characterized by exploratory movements of the head, irregular bending of the body around local supports, and movements in the rostral or caudal directions. The transition from swimming to crawling in a pegboard of variable spacing is quite distinct (Rovainen 1976a and unpublished data). Crawling behavior may depend substantially on a local myotomal reflex initiated by mechanical stimulation of the skin (Teräväinen and Rovainen 1971b). A third type of behavior involving the myotomal muscles is coiling or lashing behavior initiated after the head is grasped (Rovainen 1976a). Coiling behavior probably depends substantially on descending activity from the brain.

ORGANIZATION OF MYOTOMAL MUSCLES IN LAMPREYS

Muscle fibers in the myotomes of large ammocoetes and of adult lampreys are organized in layers of special subunits, which have not been observed in any other animals (reviews: Bone 1964; Rovainen 1979b). Each horizontal subunit extends over the length of the segment and from the medial to the lateral borders of the myotome. All myotomal muscle fibers are oriented along the longitudinal axis of the lamprey. Several horizontal layers of central muscle fibers lie in the interior of the subunit, and parietal muscle fibers cover most of the outside of it (Peters and MacKay 1961). Physiologically, the central fibers are of the twitch type, with action potentials and rapid contractions, while the parietal fibers are of the slow type with multiple innervation, high membrane resistance, slow contractions produced by synaptic potentials, and absence of action potentials (Teräväinen 1971). Although both types of muscle fibers are striated, the parietal fibers have more lipid droplets and mitochondria and less well-developed T-system and sarcoplasmic reticulum than do the central fibers (Teräväinen 1971; Lie 1974). The histochemical reactions of several enzymes are also greater in parietal than in central fibers (Meyer 1979). The organization of myotomes in recently hatched *L. japonica* is simpler than in older animals. Flat, undifferentiated muscle cells are stacked vertically in each myotomal segment and are innervated medially (Nakao 1976a, b). In large *L. lamottenii* ammocoetes one flattened central muscle cell in a subunit usually extends from the medial to the lateral edges of the myotome and perhaps is retained from the early larval stages. In small adult *P. marinus* the central muscle cells are divided into separate parallel fibers, although these remain electrotonically coupled to one another (Teräväinen 1971). Only the central fibers at the medial surface of the subunit are innervated in *P. marinus* and *L. lamottenii*, but action potentials spread rapidly through the electrotonic junctions to the rest of the twitch fibers in the subunit. As in other vertebrates, neuromuscular transmission to both parietal and central fibers in lampreys is mediated chemically and is blocked by curare (Teräväinen 1971). Two types of nerve terminals have been observed on central fibers of *L. fluviatilis* with electron microscopy (Sakharov and Kashapova 1979).

MYOTOMAL MOTONEURONS

Motoneurons in the lamprey spinal cord have been well studied anatomically and physiologically (review: Rovainen 1979b). Classically, spinal motoneurons were identified by tracing their axons into ventral roots (Tretjakoff 1909a), but more recently they have been identified anatomically by labeling after peroxidase injection into muscle (Tang and Selzer 1979). Motoneurons have been identified physiologically by intracellular stimulation with a microelectrode to produce visible contractions in the myotomes and by antidromic stimulation in *P. marinus* (Teräväinen and Rovainen 1971a) and by antidromic stimulation in *L. fluviatilis* (Batueva and Shapovalov 1974, 1977). Separate motoneurons innervate the slow and twitch muscle fibers of the ipsilateral myotomes. The slow motoneurons which activate slow fibers in *P. marinus* are smaller in size and are more numerous than the fast motoneurons which innervate twitch fibers (Teräväinen and Rovainen 1971a). Both types of motoneurons receive qualitatively similar synapses from sensory pathways (Teräväinen and Rovainen 1971b), from reticulospinal axons (Rovainen 1974b), and from vestibulospinal tracts (Rovainen 1979a). Many of the synaptic potentials in myotomal motoneurons of *P. marinus* (Rovainen 1974b, 1979a) and of *L. fluviatilis* (Batueva and Shapovalov 1977; Shapovalov 1977) are produced by electrotonic or by combined electrotonic-chemical transmission. Spinal motoneurons in *L. fluviatilis* are also electrotonically coupled to one another (Tamarova 1978).

Motoneurons to the dorsal fin muscles have also been identified physiologically. Fin motoneurons in *P. marinus* differ from myotomal motoneurons with respect to their orientation of dendrites after dye injections (Rovainen and Birnberger 1971), their participation in different reflexes (Birnberger and Rovainen 1971), and their synaptic inputs from reticulospinal axons (Rovainen 1974b). Both slow and twitch muscle fibers are present in the dorsal fins of *P. marinus*, but separate motoneurons to the two types have not been identified. Twitch muscle fibers are also present in the dorsal fins of *L. lamottenii* ammocoetes (Teräväinen 1971). In large adult sea lampreys the fins are stiffened with connective tissue and probably do not move much in relation to the body. However, in small adults fin motoneurons may contribute to swimming and orientation, and in small nonparasitic species, the fins may be used actively during spawning behavior.

GENERATION OF SWIMMING ACTIVITY IN THE SPINAL CORD

In all vertebrates which have been tested, the spinal cord itself can generate the patterned activities for limb or body movements during locomotion (review: Grillner 1975). Circuits of interneurons are assumed to produce these activities but have not been identified in fish or mammals. However, generator interneurons have been identified in the leech, and the neurophysiology of swimming in this animal has been elegantly described (Stent et al. 1978). Spinal neurons can also generate swimming activity in lampreys. Steady electrical stimulation of the isolated spinal cord of *L. fluviatilis* elicits periodic discharges of motor axons in ventral roots (Wallén 1977; Cohen and Wallén 1978), and application of acidic amino acids or L-3,4-dihydroxyphenylalanine (L-DOPA) to isolated spinal cord–myotome preparations of *I. unicuspis* elicits swimming movements and patterned activities in body muscles (Poon 1980). However, the neurons which generate these activities have not been identified.

Three types of large interneurons have been identified physiologically and anatomically and have been studied extensively in the spinal cord of *P. marinus* (Rovainen 1974a, 1979b, review). Giant interneurons are the largest nerve cells in the caudal spinal cord, they are excited by sensory pathways from the skin, and they project to the rostral spinal cord and to the brain (Rovainen 1967b, 1974a, b). Giant interneurons are not directly involved in swimming behavior (Teräväinen and Rovainen 1971b). Edge cells have an unusual location in the lateral tracts of the spinal cord, and some of them project to the contralateral side and inhibit other spinal interneurons (Rovainen 1974a). Different types of crossed inhibitory interneurons are probably present in the lamprey and are necessary for coordinating the alternate contractions of myotomes on the two sides of the body. Lateral interneurons are large cells in the rostral spinal cord, and they project caudally and inhibit a fraction of the motoneurons and other nerve cells on the same side. The hypothesis was proposed that lateral interneurons help produce undulatory postures and thus may be involved in swimming (Rovainen 1974a). Other types of interneurons have been identified anatomically in the lamprey spinal cord (Tretjakoff 1909a; Selzer 1979a; Tang and Selzer 1979) but have not been tested physiologically.

SENSORY NEURONS IN THE SPINAL CORD

Sensory activity is not necessary for the generation of locomotion in mammals or fish but can produce changes in frequency, intensity, and direction of movements. For instance, in the curarized spinal dogfish passive movement of the tail can entrain spinal generators and change the frequency of discharges in motoneurons (Grillner and Wallén 1977). Conversely, cutaneous reflexes in the dogfish tail are modified appropriately according to the phase of swimming (Grillner et al. 1977). Such experiments have not been extended to the lamprey, but the ability of ammocoetes and adults to swim through narrow spaces indicates that they can use sensory feedback to modify swimming movements.

Two types of sensory neurons project into the lamprey spinal cord. Dorsal root ganglion cells are the most numerous type, but because of technical difficulties their physiology has not been investigated. The other type of sensory neuron, the dorsal cell, is well known from anatomical and physiological studies. Sigmund Freud (1877, 1888) demonstrated histologically that the axons of dorsal cells in *L. planeri* and *P. marinus* project in dorsal roots. His observations were later confirmed by electrical recording and stimulation and by injection of dyes into dorsal cells (Rovainen 1976b; Martin and Wickelgren 1971). The physiological properties of dorsal cells are similar in adult *P. marinus* (Rovainen 1967b; Martin and Wickelgren 1971), in adult *I. unicuspis* (Selzer 1979b), and in *L. planeri* and *L. fluviatilis* ammocoetes (Martin and Bowsher 1977). Dorsal cells respond to mechanical stimulation of the skin and can be classified as touch, pressure, and nociceptive types. The three functional types of dorsal cells also have different electrical properties (Martin and Wickelgren 1971). Dorsal cells do not exhibit synaptic potentials after spinal stimulation (Rovainen 1967b; Martin and Wickelgren 1971; Martin and Bowsher 1977) and do not respond to putative transmitters (Martin et al. 1970; Homma and Rovainen 1978b). The central axons of dorsal cells project in the dorsal tracts into the rostral spinal cord (Rovainen 1967b) and as far as the isthmic region of the brain (Martin and Bowsher 1977). Rohon–Beard cells, which are homologous to dorsal cells in the lamprey, occur transiently during the development of fish and amphibians (review: Hughes 1957). The only nerve fibers which innervate the skin in *Xenopus* embryos are those from Rohon–Beard cells, and electrical recordings from these fibers show that they are excited by touch stimuli to the skin (Roberts and Hayes 1977).

MULLER AND MAUTHNER CELLS

The most important descending pathway from the brain to the spinal cord of the lamprey is the reticulospinal system which consists of a few dozen giant nerve cells and axons. The anatomical and physiological properties of these neurons have been reviewed in detail (Rovainen 1978, 1979b). The dendritic fields of these cells have also been described after dye injections (Martin 1979). The outstanding feature of the Müller and Mauthner neurons is that they can be recognized individually in different animals by the positions of their visible cell bodies in the brain and of their axons in the spinal cord. Such individually identified neurons are extremely infrequent in the vertebrate central nervous system, the best known example being the Mauthner cell in fish and amphibians. Since the Müller and Mauthner neurons in the lamprey can be tested repeatedly for synaptic connections with other nerve cells, it has been possible to determine a simple though incomplete circuit diagram for the reticulospinal system (Rovainen 1974b). The general function of the reticulospinal Müller and Mauthner cells is excitation of spinal motoneurons and interneurons during arousal from various sensory stimuli. However, the individual Müller and Mauthner neurons differ from one another in their detailed synaptic connections and in the types of motor responses they promote, as described briefly below.

The Mauthner neurons in the lamprey brain have been identified on the basis of the positions of their cell bodies near the vestibular nerves and of their crossed axons in the lateral spinal cord (Whiting 1957; Rovainen 1967a; Rovainen et al. 1973). Like the

Mauthner cell in teleost fish, the anterior Mauthner cell in *P. marinus* and in other species of lampreys is excited by vibrations of the labyrinths and by monosynaptic electrotonic transmission from vestibular afferents (Rovainen 1979a). The Mauthner cells in both teleosts and lampreys are also excited after stimulation of other cranial nerves, particularly the posterior lateral line nerves. However, the Mauthner cell in lampreys differs from the cell in teleosts by its lack of strong inhibition either from the paired cell or from the contralateral vestibular nerve (Rovainen 1979a, b). Strong inhibition is not required in the lamprey because activity in the Mauthner cell does not produce pronounced movements in the animal. Repetitive intracellular stimulation of the Mauthner axon in ammocoetes of *P. marinus* elicits weak backwards crawling movements and, in small adults, movements of the dorsal fins (Rovainen 1967a). The Mauthner axons make excitatory synapses on myotomal motoneurons and on unidentified interneurons in the lamprey spinal cord (Rovainen 1974b).

The Müller neurons in the lamprey are identified by the positions of their cell bodies in the midbrain and medulla and of their uncrossed axons in the ventral spinal cord (Rovainen 1967a; Rovainen et al. 1973). Many of the Müller axons make combined electrotonic and chemical synapses on myotomal motoneurons on the same side (Rovainen 1974b; Batueva and Shapovalov 1977). Müller cells in the bulbar group also make similar excitatory synapses on lateral interneurons in the spinal cord (Rovainen 1974b; Ringham 1975). The Müller cells are excited and inhibited by a variety of sensory stimuli (Wickelgren 1977a). The activities of some cells are related to specific behavior, for instance, M_3 and I_1 are excited by certain directions of rotations of the vestibular labyrinths, and in turn they promote movements of the dorsal fins for righting responses (Rovainen 1979a). One pair of Müller neurons (I_2) has an unusual sensory function. The I_2 axons receive excitatory synapses in the spinal cord (Rovainen 1964a: 1974b; Kershaw and Christensen 1980) and are excited after the skin of the body and tail is touched or brushed (Teräväinen and Rovainen 1971b; Rovainen 1974b). The I_2 cell bodies can also generate action potentials, particularly after stimulation of the posterior lateral line nerves (C. Rovainen unpublished data). The I_2 axons make combined electrotonic and chemical synapses on giant interneurons in the spinal cord (Rovainen 1967b; Christensen and Teubl 1979b) and help excite these neurons during stimulation of the tail. Giant interneurons in turn excite the Müller cell B_3 in the brain. An unidentified Müller axon of the bulbar group produces weak swimming movements during intracellular stimulation (Rovainen 1967a).

The third type of reticulospinal neuron in the lamprey has an uncrossed axon in the lateral spinal cord (Rovainen 1967a; Rovainen et al. 1973). The V cells in the caudal medulla are the most important neurons in this group. One known function of the V cells and other lateral reticulospinal neurons is their participation in vestibulospinal reflexes (Rovainen 1979a, and next section).

VESTIBULAR SYSTEM

Normal swimming in ammocoetes and adult lampreys depends substantially upon the vestibular system. After removal of the labyrinthine membranes from both otic capsules, adult lampreys (*L. fluviatilis*) swim upside down or sideways with quick and frequent turns in all directions. Removal of the labyrinthine membranes from only one of the capsules produces swimming in spirals towards the injured side and deviations in the positions of the eyes (de Burlet and Versteegh 1930). Similar behavior deficits occur after labyrinthectomy in *P. marinus* ammocoetes (Rubinson 1974) and in adult *P. marinus* (Rovainen 1976b) and *I. unicuspis* (C. Rovainen unpublished data).

The vestibular system of lampreys has been studied physiologically and appears to have similar properties in various species. Lowenstein (1970) determined the responses of groups of vestibular afferents to rotations, tilts, and vibrations of the isolated otic capsule of adult *L. fluviatilis*. Excitatory and inhibitory directions of rotations correlate well with the orientations of sensory hair cells (Lowenstein et al. 1968). Some fibers in the anterior vestibular nerve are particularly responsive to vibrations (Lowenstein 1970). Electrical stimulation of the vestibular nerves elicits coordinated and appropriate movements of the eyes (Rovainen 1976b) and of the head (Rovainen 1979a). Head movements are promoted by disynaptic excitation of myotomal motoneurons through the vestibulospinal tracts and, more importantly, by recruitment of reticulospinal V neurons with axons in the lateral tracts (Rovainen 1979a). The lateral reticulospinal neurons in adult *P. marinus* and *I. unicuspis* respond strongly to specific rotations of the labyrinths around one, two, or three different axes (Rovainen 1979a). In turn, the reticulospinal cells excite myotomal motoneurons in both the neck and body regions (Rovainen 1974b) and promote movements of the body and fins (Rovainen 1967a). Lateral interneurons in the spinal cord are also excited by activity in reticulospinal neurons (Rovainen 1974b) and in the vestibulospinal tracts (Rovainen 1979a). Perhaps these interneurons help coordinate swimming and vestibulospinal reflexes. The large Müller and Mauthner cells in adult *P. marinus* and *I. unicuspis* and in *L. lamottenii* ammocoetes also respond to vestibular stimulation. The cells M_3 and I_1 are specifically excited by upward rotation of the nose and by downward rotation of the contralateral otic capsule (Rovainen 1979a). Intracellular stimulation of M_3 and I_1 in adult *P. marinus* produces movements of the dorsal fins to the opposite side (Rovainen 1967a, 1974b), the appropriate response for righting following axial rotation. In contrast, the Mauthner neurons are excited by vibrations, and the Müller cells of the bulbar group by a variety of vestibular stimuli, as part of a general arousal response.

AROUSAL AND ORIENTATION

One way in which sensory systems in the lamprey contribute to swimming is arousal of the animal. In isolated preparations of adult lampreys and ammocoetes the brain and spinal cord show little spontaneous activity, except for respiratory discharges (see next section). However, electrical or natural stimulation of a variety of sensory systems produces long periods of synaptic activity in reticulospinal neurons (Wickelgren 1977a, b) and discharges in their axons. In intact animals the descending discharges from the brain are accompanied by swimming or crawling movements. The late activities or afterdischarges in reticulospinal neurons are apparently produced by a recurrent excitatory system in the brain. The recurrent system receives excitatory input from all major sensory systems and in turn excites reticular cells and promotes transmission through sensory pathways. The neurons, synapses, and any special physiological mechanisms of the recurrent system are unknown (Wickelgren 1977a, b). Arousal can lead to escape or to attack behavior, but the neurophysiology of the two different behavioral states in the lamprey has not been investigated.

Guidance is another function of sensory systems once swimming has been initiated. The neurophysiology of orientation in lampreys is unknown, except for some responses produced by the vestibular system (previous section). The well-developed eyes of adult lampreys suggest that patterned vision is present in these animals, but responses of individual neurons in the retina or optic tectum have not been tested with standard spots, lines, and moving edges. Responses to light flashes have been recorded in the tectum (Veselkin 1966) and in reticulospinal neurons (Wickelgren 1977a) and would be expected to produce arousal. However, patterned vision would be much more useful than responses to illumination for correction of body position or for perception of prey and other objects. Water currents could provide important sensory cues to adult lampreys for upstream and downstream migrations, for detection of moving objects in the water, and for selection of nesting sites. At present, little behavioral and no physiological evidence indicates that receptors for water currents are present in lampreys. No specific responses to fluid movement over neuromasts were observed during initial recordings from sensory neurons (Matthews and Wickelgren 1978a). In higher fish the senses of hearing (Tavolga 1971) and of electroreception (Bennett 1971; Fessard 1974) are well developed. D. Bodznick and R. G. Northcutt (Univ. Mich., Ann Arbor, personal communication) have recorded responses in the tectum and medulla of adult *E. tridentatus* to weak electric fields along the body. Fish odors arouse parasitic *P. marinus* and produce increased swimming activities (Kleerekoper and Morgensen 1963). *Petromyzon marinus* adults are also attracted or repelled by water in which other lampreys have been kept (Teeter 1980).

In conclusion, swimming in lampreys involves myotomal muscles, spinal cord, brain, and sensory systems. The physiology of muscles, motoneurons, reticulospinal neurons, and the vestibular system are rather well understood. Some important goals for future research are the identification of spinal generators, the determination of mechanisms for arousal, and the behavioral and physiological investigation of sensory systems, especially vision.

Neurophysiology of Breathing

Respiration is one of the most important functions dependent upon the nervous system in lampreys. Both ammocoetes and adult lampreys have well-developed gills, and the rates of oxygen consumption in adults are not very different from higher fish (review: Lewis 1980). The general mechanisms (review: Randall 1972) and neural control (review: Rovainen 1977) of breathing in ammocoetes and adult lampreys are well known. The ventilation of ammocoetes is unidirectional and is produced by periodic contractions of the velum and of the branchial muscles (Rovainen and Schieber 1975). In adult lampreys the attachment of the sucker mouth to a rock or fish prevents water from entering the mouth. Instead, water moves alternately in and out of the gill sacs through the gill openings (Dawson 1905; Roberts 1950). Both in ammocoetes (Homma 1975; Rovainen and Schieber 1975) and in adult lampreys (Roberts 1950; Rovainen 1974c) the muscles of the branchial basket contract synchronously for active exhalation of water from the gill chambers. The phase of inhalation is passive as the branchial basket expands elastically and draws water into the gill chambers through the gill openings in adults or through the mouth in ammocoetes.

BRANCHIAL MOTONEURONS

Motoneurons to the respiratory muscles of the branchial basket have been identified physiologically in adult lampreys (Rovainen 1974c) and in ammocoetes (Homma 1975). The vagus (X) is the major motor nerve to the branchial muscles in *P. marinus*, *I. castaneus*, and *L. aepyptera*. Additional motor axons in the cranial nerves VII and IX innervate the most rostral branchial muscles. Motoneurons located in the ipsilateral IX and X motor nuclei in the medulla have been identified by intracellular stimulation and observation of visible contractions in the branchial muscles and by antidromic stimulation (Rovainen 1974c; Homma 1975). Neuromuscular transmission to the branchial muscles in lampreys is probably cholinergic, since respiratory movements cease in curarized preparations (Wickelgren 1977a). The cranial motor nuclei and nerves also stain positively for cholinesterase (Wächtler 1974).

VELAR MOTONEURONS

The velum is the major respiratory pump in ammocoetes, and the motoneurons which drive it have been identified in the trigeminal nucleus. After the branchial muscles have been paralyzed by cutting the IX–X nerves in *P. marinus* ammocoetes, the continuing activity of the velum produces nearly normal resting ventilation. Conversely, disruption of velar contractions by sectioning the trigeminal (V) nerve either killed the ammocoete or reduced ventilation severely (Rovainen and Schieber 1975). During normal breathing of ammocoetes the velar pouches initiate the ventilatory cycle by contracting backward and forcing water from the pharynx through the gills. Near the end of velar activity the branchial muscles contract and enhance stroke volume by compressing the gill chambers. The final phase of the cycle is passive, as the valves over the gill openings close, the branchial basket recoils, and water is drawn between the relaxing velar pouches into the gill sacs (Rovainen and Schieber 1975). The velum contains unusual "tubular" striated muscle fibers (review: Rovainen 1979b) with slow contraction times and ultrastructural properties similar to those of the muscle fibers of the craniovelaris muscle in the hagfish (Korneliussen 1973; Korneliussen and Nicolaysen 1973, 1975). The muscle fibers in the velum of ammocoetes and of hagfish are innervated by motor fibers in the trigeminal nerve. Motoneurons to the velum in ammocoetes of *P. marinus*, *L. aepyptera*, and *L. lamottenii* have been identified physiologically by intracellular stimulation and by antidromic stimulation and are located in the lateral part of the trigeminal nucleus on the same side (Homma 1975, 1978). The timing of excitatory synaptic potentials and of the firing of velar motoneurons during the respiratory cycle (Homma 1975) corresponds well to the observations of movements described above. During metamorphosis the velum becomes smaller and changes its function from a respiratory pump to a valve between the pharynx and water tube of the adult lamprey. Motoneurons to the velum in adult *L. aepyptera*, *L. lamottenii*, and *I. unicuspis* have also been identified physiologically in the lateral part of the trigeminal nucleus (Homma 1978).

GENERATION OF RESPIRATORY DISCHARGES

Patterned activity for breathing in lampreys is generated in the brain stem. The periodic discharges in motoneurons and in branchial muscles of adult *P. marinus*, *I. castaneus* (Rovainen 1974c), *I. unicuspis* (Rovainen 1977), *L. fluviatilis* (Roberts 1950), and *L. japonica* (Kawasaki 1979) consist of brief, synchronous bursts which precede each compression of the branchial basket. No activity of possible antagonist muscles has been recorded. Motoneurons to the various types of branchial muscles are driven by powerful bursts of synaptic potentials from generator neurons. Sensory neurons are not the generators, since bursts of potentials continue in the isolated lamprey brain. The motoneurons themselves do not initiate the respiratory rhythm, as judged by various physiological tests (Rovainen 1974c). The synaptic excitation of branchial motoneurons in ammocoetes of *P. marinus* and *L. aepyptera* is similar to that in adults. However, the velar motoneurons are driven by an earlier and more prolonged phase of synaptic potentials, also produced by generators within the brain stem (Homma 1975). Lesions of the brain in ammocoetes and adult lampreys indicate that the respiratory generators lie in the medulla and that a pathway coordinating the activities on both sides crosses the midline between the trigeminal nuclei (Rovainen 1974c; Homma 1975; Kawasaki 1979). In ammocoetes the generator for velar excitation lies near the trigeminal nucleus and entrains ipsilateral branchial excitation (Homma 1975). In adult lampreys the generators may lie caudal to the trigeminal nucleus (Kawasaki 1979). Lesions of the spinal cord and forebrain have no effect on respiratory discharges, but cutting the brain stem between the midbrain and the medulla sometimes depresses activity (Rovainen 1977; Kawasaki 1979). Generation of respiratory activities can still continue in both halves of the brain stem after midline sections in adult *L. japonica* (Kawasaki 1979).

Generator neurons have not been identified in the lamprey, but some of their physiological properties have been inferred from changes in frequency of respiratory discharges in the isolated brains of adult *I. unicuspis* (Rovainen 1977). Changes in external Ca^{++} and Mg^{++} probably affect the thresholds for firing of generator neurons, since frequencies of respiratory bursts in the IX–X nerves increase in low Ca^{++} and decrease in elevated concentrations of Ca^{++} or Mg^{++}. Increased external K^+ usually depresses breathing frequency, perhaps by enhancing postspike inexcitability. Shifts in pH produced by changes in CO_2 and HCO_3^- do not produce strong or consistent changes in the frequency of respiratory discharges from the isolated lamprey brain. Although exposure of the isolated brain to 100% O_2 can depress breathing frequency, bathing it in N_2-equilibrated fluid does not increase the frequency of discharges (Rovainen 1977). Temperature appears to be the most important factor which directly affects the central generation of respiratory discharges. In intact ammocoetes and adult lampreys (Potter et al. 1970; Johansen et al. 1973; Claridge and Potter 1975; Rovainen and Schieber 1975) and in the isolated brain (Rovainen 1977) low temperatures decrease the frequencies of breathing and high temperatures increase them. The direct excitatory effect of increased temperature on respiratory generators in the brain may have the useful function of anticipating the increased metabolic requirements of the animal prior to the sensory feedback from O_2 receptors.

MODIFICATION OF BREATHING BY MECHANO- AND CHEMO-RECEPTORS

Breathing behavior of adult lampreys and of ammocoetes can be modified by sensory systems. Low levels of oxygen increase the frequency of breathing in adult *L. fluviatilis* (Claridge and Potter 1975), in adult *E. tridentatus* (Johansen et al. 1973), in *I. hubbsi* ammocoetes (Potter et al. 1970), and in *P. marinus* ammocoetes (Rovainen and Schieber 1975). Low oxygen also markedly increases the ventilation volume of *P. marinus* ammocoetes, predominant by increasing stroke volume (Rovainen and Schieber 1975). In adult *L. fluviatilis* oxygen consumption also increases in low oxygen, perhaps as a consequence of increased breathing activity (Claridge and Potter 1975). High levels of oxygen depress breathing frequency in adult *E. tridentatus* (Johansen et al. 1973) and decrease ventilation in *P. marinus* ammocoetes (Rovainen and Schieber 1975). Receptors for low oxygen have not been identified in the lamprey but appear to be situated within the body. The brain is an unlikely receptor site since it does not respond to low O_2 in vitro (Rovainen 1977). The skin and external surfaces of the gills are also unlikely sites for oxygen receptors, since ammocoetes continue to breathe vigorously for many minutes in normal aerated water following obstruction of ventilation (Rovainen and Schieber 1975). Sectioning the IX–X nerves in *P. marinus* ammocoetes reduces their hyperventilation after obstruction, but this may be due to motor and/or sensory deficits (Rovainen and Schieber 1975). The breathing of fish depends less upon pH and levels of CO_2 than does that of air-breathing animals. Nevertheless, *I. hubbsi* ammocoetes emerge from burrows and breathe more rapidly after exposure to water with lowered pH produced by bubbling with CO_2 (Potter et al. 1970). Low pH may produce a general arousal or alteration of the metabolism of ammocoetes and consequently an indirect increase in respiration.

Mechanoreceptive afferents have been recorded in the IX–X nerves of adult *I. unicuspis* (Rovainen 1977). Some of these respond to touching the gill openings, to pressure on the branchial basket on either side, or to increases in blood pressure in the gills. "Cough" reflexes are also produced by touching the gill openings and by increasing internal gill pressure. "Coughs" consist of intense, prolonged, bilateral contractions of the branchial muscles, which blow water and irritating particles from the gill openings. Repetitive electrical stimulation of a IX–X nerve root can also elicit bilateral "cough" discharges in other roots of the isolated brain of adult *I. unicuspis* (C. Rovainen unpublished data). Both adult lampreys (Dawson 1905) and ammocoetes also have forward coughing responses for detachment or for dislodging particles in the mouth. In *P. marinus* ammocoetes, increased pressure on the branchial basket relative to the mouth increases the mechanical load against breathing and depresses the frequency of breathing (Rovainen and Schieber 1975). The mechanoreceptors which mediate this response have not been identified but may be situated in or near the velum and may project in the trigeminal nerve.

Respiratory neurons in the lamprey are recruited during arousal responses and therefore respond indirectly to a variety of additional sensory stimuli. During crawling and swimming the branchial basket is contracted tonically and ventilatory movements cease in ammocoetes (Rovainen and Schieber 1975) and in small adult lampreys. Following arousal responses in the isolated brain, periodic respiratory bursts reappear and are stronger than normal for several cycles (C. Rovainen unpublished data). Thus the increased ventilation following locomotion in ammocoetes (Rovainen and Schieber 1975) and in adult lampreys may be produced in part by stronger intrinsic activity in the brain and in part by metabolic debt and feedback from peripheral oxygen receptors.

Conclusions: Prospects in Lamprey Neurophysiology

Various problems in lamprey neurophysiology are attractive for future research. Neuroanatomy, cellular neurophysiology, and systems for swimming and respiration are well known but still have many important unanswered questions. The functions of sensory systems in the lamprey are poorly understood. In particular, behavioral tests and unit recordings should be used to study patterned vision in adult lampreys. Behavioral responses of adults to water currents, weak electric fields, and sound should also be tested. The central mechanisms by which sensory stimuli arouse lampreys are unknown and should be investigated further. The major motor system which has not been studied in detail neurophysiologically is feeding, one of the most distinctive and complicated behaviors of adult parasitic lampreys. Attachment reflexes could be studied in isolated preparations, and behavioral tests on intact adults could be used to determine the effects of olfaction and taste on feeding. The spawning behavior of adult lampreys is well known but has not been investigated neurophysiologically.

Long-term control of sea lamprey populations in the Great Lakes depends upon continuing research, both basic and targeted. Fundamental information on the biology of lampreys can provide new ideas for possible control methods, and general knowledge can be used to judge which methods are most likely to be successful. No clear ideas for lamprey control emerge from the present information on the lamprey nervous system. Future neurophysiological research should concentrate on *P. marinus*, since this species is the target for control and is also the species best suited for most experiments on the nervous system.

AHLBORN, F. 1883. Untersuchungen über das Gehirn der Petromyzon. Z. Wiss. Zool. Abt. A, 39: 191–294.

ARIËNS KAPPERS, C. U. 1926. The meninges in lower vertebrates compared with those in mammals. Arch. Neurol. Psychiat. 15: 281–296.

Balabai, P. P. 1946. Metamorphosis of the visceral apparatus of the lamprey. C. R. (Dokl.) Acad. Sci. URSS 53: 765–768.

Batueva, I. V., and A. I. Shapovalov. 1974. Synaptic effects evoked by supraspinal and intraspinal stimulation in lamprey motoneurons. Neurophysiology (Transl.) 6: 500–505.

1977. Synaptic effects evoked in motoneurons by direct stimulation of single presynaptic fibers in the lamprey. Neurophysiology (Transl.) 9: 301–305.

Baumgarten, H. G. 1972. Biogenic amines in the cyclostome and lower vertebrate brain. Prog. Histochem. Cytochem. 4: 1–90.

Beamish, F. W. H. 1974. Swimming performance of adult sea lamprey, *Petromyzon marinus*, in relation to weight and temperature. Trans. Am. Fish. Soc. 103: 355–358.

Bennett, M. V. L. 1971. Electroreception, p. 493–574. *In* W. S. Hoar and D. J. Randall [ed.] Fish Physiology, Vol. 5. Academic Press, NY.

Bertolini, B. 1964. Ultrastructure of the spinal cord of the lamprey. J. Ultrastruct. Res. 11: 1–24.

Bertolini, B., and F. Mangia. 1966. Osservazioni sulla ultrastruttura dell'occhio pineale della lampreda. Accad. Naz. Lincei, Rome. Cl. Sci. Fis. Mat. Nat. Rend. 41: 147–153.

Birnberger, K. L., and C. M. Rovainen. 1971. Behavioral and intracellular studies of a habituating fin reflex in the sea lamprey. J. Neurophysiol. 34: 983–989.

Bone, Q. 1964. Patterns of muscular innervation in the lower chorates. Int. Rev. Neurobiol. 6: 99–147.

Bruckmoser, P. 1971. Elektrische Antworten im Vorderhirn von *Lampetra fluviatilis* (L.) bei Reizung des Nervus olfactorius. Z. Vergl. Physiol. 7: 69–85.

Christensen, B. N. 1976. Morphological correlates of synaptic transmission in lamprey spinal cord. J. Neurophysiol. 39: 197–212.

Christensen, B. N., and J. Quinn. 1979. The relationship between some measures of synaptic ultrastructure as a function of distance from the soma on lamprey reticulospinal neurons. J. Neurocytol. 8: 737–750.

Christensen, B. N., and W. P. Teubl. 1979a. Estimates of cable parameters in lamprey spinal cord neurones. J. Physiol. (London) 297: 299–318.

1979b. Localization of synaptic input on dendrites of a lamprey spinal cord neurone from physiological measurements of membrane properties. J. Physiol. (London) 297: 319–333.

Claridge, P. N., and I. C. Potter. 1975. Oxygen consumption, ventilatory frequency and heart rate of lampreys (*Lampetra fluviatilis*) during their spawning run. J. Exp. Biol. 63: 193–206.

Cohen, A. H., and P. Wallén. 1978. Rhythmic locomotor activity induced in an *in vitro* preparation of the lamprey spinal cord. Neurosci. Lett., Suppl. 1: 92.

Collin, J.-P. 1968. L'épithélium sensoriel de l'organe pinéal de la larve âgée et de l'adulte de *Lampetra planeri*. C. R. Acad. Sci. Ser. D, 267: 1768–1771.

1969. La cupule sensorielle de l'organe pinéal de la lamproie de planer. L'ultrastructure des cellules sensorielles et ses implications fonctionnelles. Arch. Anat. Microsc. Morphol. Exp. 58: 145–182.

Collin, J.-P., and A. Meiniel. 1968a. Les synapses de l'organe pinéal de l'ammocète. C. R. Acad. Sci. Ser. D, 266: 1293–1295.

1968b. Contribution à la connaissance des structures synaptiques du type ruban dans l'organe pinéal des vertébrés. Étude particulière en microscopie électronique des connexions de l'innervation efférente chez l'ammocète de lamproie de planer. Arch. Ant. Microsc. Morphol. Exp. 57: 275–296.

Damas, H. 1935. Contribution à l'étude de la métamorphose de la tête de la lamproie. Arch. Biol. 46: 171–227.

1944. Recherches sur le développement de *Lampetra fluviatilis* L. Contribution à l'étude de la céphalogenèse des vertébrés. Arch. Biol. 55: 1–284.

Dawson, J. 1905. The breathing and feeding mechanism of the lampreys. II. Food and mechanism of feeding. III. Mechanism of respiration. Biol. Bull. 9: 91–111.

de Burlet, H. M., and C. Versteegh. 1930. Ueber Bau und Funktion des Petromyzonlabyrinthes. Acta Oto-Laryngol. Suppl. 13: 5–58.

Dickson, D. H., and T. R. Collard. 1979. Retinal development in the lamprey (*Petromyzon marinus* L.): premetamorphic ammocoete eye. Am. J. Anat. 154: 321–336.

Dickson, D. H., and D. A. Graves. 1979. Fine structure of the lamprey photoreceptors and retinal pigment epithelium (*Petromyzon marinus* L.). Exp. Eye Res. 29: 45–60.

Dreyfert, T., K. Holmberg, and G. Struwe. 1979. Critical fusion frequency of the river lamprey (*Lampetra fluviatilis*). Vision Res. 19: 551–553.

Eddy, J. M. P. 1972. The pineal complex, p. 91–103. *In* M. W. Hardisty and I. C. Potter. [ed.] The biology of lampreys. Vol. 2. Academic Press, London.

Ehinger, B., K. Holmberg, and P. Öhman. 1977. Aminergic and indoleamine accumulating neurons in the retina of the river lamprey (*Lampetra fluviatilis*). Acta Zool. (Stockholm) 58: 117–123.

Fernholm, B., M. Nielsen, and C. Braestrup. 1979. Absence of brain specific benzodiazepine receptors in cyclostomes and elasmobranchs. Comp. Biochem. Physiol. C, 62: 209–211.

Fessard, A. 1974. Electroreceptors and other specialized receptors in lower vertebrates, p. 1–256. Handbook of Sensory Physiology, Vol. III/3. Springer-Verlag, Berlin.

Finger, T. E., and C. M. Rovainen. 1978. Retrograde HRP labeling of the oculomotoneurons in adult lampreys. Brain Res. 154: 123–127.

Freud, S. 1877. Über den Urspring der hinteren Nervenwurzeln im Rückenmark von Ammocoetes (Petromyzon Planeri). S. B. Akad. Wis. Wien. 75: 15–30.

1878. Über Spinalganglien und Rückenmark des Petromyzon. S. B. Akad. Wis. Wien. 78: 81–167.

Gage, S. H. 1917. Glycogen in the nervous system of vertebrates. J. Comp. Neurol. 27: 451–465.

Gorbman, A. 1980. Evolution of the brain–pituitary relationship: evidence from the Agnatha. Can. J. Fish. Aquat. Sci. 37: 1680–1686.

Grillner, S. 1975. Locomotion in vertebrates: central mechanisms and reflex interaction. Physiol. Rev. 55: 247–304.

Grillner, S., and S. Kashin. 1976. On the generation and performance of swimming in fish, p. 181–201. *In* R. M. Herman, S. Grillner, P. S. G. Stein, and D. G. Stuart [ed.]. Neural control of locomotion. Plenum, NY.

Grillner, S., S. Rossignol, and P. Wallén. 1977. The adaptation of a reflex response to the ongoing phase of locomotion in fish. Exp. Brain Res. 30: 1–11.

Grillner, S., and P. Wallén. 1977. Is there a peripheral control of the central pattern generators for swimming in dogfish? Brain Res. 127: 291–295.

Healey, E. G. 1972. The central nervous system, p. 307–372.

In M. W. Hardisty and I. C. Potter [ed.]. The biology of lampreys. Vol. 2. Academic Press, London.

Heier, P. 1948. Fundamental principles in the structure of the brain. A study of the brain of *Petromyzon fluviatilis*. Acta Anat. Suppl. 8: 1–213.

Herrick, C. J., and J. B. Obenchain. 1913. Notes on the anatomy of a cyclostome brain: *Ichthyomyzon concolor*. J. Comp. Neurol. 23: 635–675.

Hibbard, E. 1963a. Regeneration in the severed spinal cord of chordate larvae of *Petromyzon marinus*. Exp. Neurol. 7: 175–185.

1963b. The vascular supply to the central nervous system of the larval lamprey. Am. J. Anat. 113: 93–99.

Holmberg, K. 1978a. Electron microscopic analysis of the inner synaptic layer in the river lamprey (*Lampetra fluviatilis*). Acta Zool. (Stockholm) 59: 107–117.

1978b. Light- and electron-microscopic investigation of the optic nerve fiber layer in the river lamprey (*Lampetra fluviatilis*). Vision Res. 18: 1313–1320.

Holmberg, K., P. Öhman, and T. Dreyfert. 1977. ERG-recordings from the retina of the river lamprey (*Lampetra fluviatilis*). Vision Res. 17: 715–717.

Homma, S. 1975. Velar motoneurons of lamprey larvae. J. Comp. Physiol. 104: 175–183.

1978. Organization of the trigeminal motor nucleus before and after metamorphosis in lampreys. Brain Res. 140: 33–42.

1979. Conductance changes during bath applications of β-alanine and taurine in giant interneurons of the isolated lamprey spinal cord. Brain Res. 173: 287–293.

Homma, S., and C. M. Rovainen. 1978. Conductance increases produced by glycine and γ-aminobutyric acid in lamprey interneurones. J. Physiol. (London) 279: 231–252.

Honma, S. 1969. Fluorescence microscopic observations on the brain of the lamprey, *Lampetra japonica*. Arch. Histol. Jap. 31: 167–178.

1970. Presence of monoaminergic neurons in the spinal cord and intestine of the lamprey, *Lampetra japonica*. Arch. Histol. Jap. 32: 383–393.

Hoshino, T. 1975. An electron microscopic study of the otolithic maculae of the lamprey (*Entosphenus japonicus*). Acta Oto-Laryngol. 80: 43–53.

Hughes, A. 1957. The development of the primary sensory system in *Xenopus laevis* (Daudin). J. Anat. 91: 323–338.

Johansen, K., C. Lenfant, and D. Hanson. 1973. Gas exchange in the lamprey, *Entosphenus tridentatus*. Comp. Biochem. Physiol. A, 44: 107–119.

Johnston, J. B. 1902. The brain of *Petromyzon*. J. Comp. Neurol. 12: 2–86.

1905. The cranial nerve components of *Petromyzon*. Morphol. Jahrb. 34: 149–203.

1912. The telencephalon in cyclostomes. J. Comp. Neurol. 22: 341–404.

Kawasaki, R. 1979. Breathing rhythm-generation in the adult lamprey, *Entosphenus japonicus*. Jpn. J. Physiol. 29: 327–338.

Keibel, F. 1927. Beiträge zur Anatomie, zur Entwicklungsgeschichte und zur Stammesgeschichte der Sehorgane der Cyklostomen. Z. Mikrosk. Anat. Forsch. 12: 391–456.

Kennedy, M. C., and K. Rubinson. 1977. Retinal projections in larval, transforming and adult sea lamprey, *Petromyzon marinus*. J. Comp. Neurol. 171: 465–479.

Kershaw, P., and B. N. Christensen. 1980. A quantitative analysis of ultrastructural changes induced by electrical stimulation of identified spinal cord axons in the larval lamprey. J. Neurocytol. 9: 119–138.

Kleerekoper, H. 1972. The sense organs, p. 373–404. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2. Academic Press, London.

Kleerekoper, H., and J. Mogensen. 1963. Role of olfaction in the orientation of *Petromyzon marinus*. I. Response to a single amine in prey's body odor. Physiol. Zool. 36: 347–360.

Konstantinova, M. 1973. Monoamines in the liquor-contacting nerve cells in the hypothalamus of the lamprey, *Lampetra fluviatilis* L. Z. Zellforsch. Mikrosk. Anat. 114: 549–557.

Korneliussen, H. 1973. Ultrastructure of motor nerve terminals on different types of muscle fibers in the Atlantic hagfish (*Myxine glutinosa*, L.). Occurrence of round and elongated profiles of synaptic vesicles and dense-core vesicles. Z. Zellforsch. Mikrosk. Anat. 147: 87–105.

Korneliussen, H., and K. Nicolaysen. 1973. Ultrastructure of four types of striated muscle fibers in the Atlantic hagfish (*Myxine glutinosa* L.) Z. Zellforsch. Mikrosk. Anat. 143: 273–290.

1975. Distribution and dimension of the T-system in different muscle fiber types in the Atlantic hagfish (*Myxine glutinosa*, L.). Cell Tissue Res. 157: 1–16.

Kosareva, A. A., N. P. Veselkin, and T. M. Ermakova. 1977. Retinal projections in the lamprey *Lampetra fluviatilis* as revealed by optic nerve transport of horseradish peroxidase. J. Evol. Biochem. Physiol. (Transl.) 13: 256–258.

Larsell, O. 1947. The cerebellum of myxinoids and petromyzonts including developmental stages in the lampreys. J. Comp. Neurol. 86: 395–445.

Leach, W. J. 1951. The hypophysis of lampreys in relation to the nasal apparatus. J. Morphol. 89: 217–255.

Lewis, S. V. 1980. Respiration of lampreys. Can. J. Fish. Aquat. Sci. 37: 1711–1722.

Lewis, S. V., and I. C. Potter. 1977. Oxygen consumption during the metamorphosis of the parasitic lamprey, *Lampetra fluviatilis* (L.) and its non-parasitic derivative, *Lampetra planeri* (Bloch). J. Exp. Biol. 69: 187–198.

Lie, H. R. 1974. A quantitative identification of three muscle fiber types in the body muscles of *Lampetra fluviatilis*, and their relation to blood capillaries. Cell Tissue Res. 154: 109–119.

Lindström, T. 1949. On the cranial nerves of the cyclostomes with special reference to n. trigeminus. Acta Zool. (Stockholm) 30: 315–458.

Lowenstein, O. 1970. The electrophysiological study of the responses of the isolated labyrinth of the lamprey (*Lampetra fluviatilis*) to angular acceleration, tilting, and mechanical vibration. Proc. R. Soc. London Ser. B, 174: 419–434.

Lowenstein, O., M. P. Osborne, and R. A. Thornhill. 1968. The anatomy and ultrastructure of the labyrinth of the lamprey (*Lampetra fluviatilis* L.) Proc. R. Soc. London Ser. B, 170: 113–134.

Manion, P. J., and T. M. Stauffer. 1970. Metamorphosis of the landlocked sea lamprey, *Petromyzon marinus*. J. Fish Res. Board Can. 27: 1735–1746.

Marón, K. 1959. Regeneration capacity of the spinal cord in *Lampetra fluviatilis* larvae. Folia Biol. (Warsaw) 7: 179–189.

Martin, A. R., and G. L. Ringham. 1975. Synaptic transfer at a vertebrate central nervous system synapse. J. Physiol. (London) 251: 409–426.

Martin, A. R., and W. O. Wickelgren. 1971. Sensory cells in the spinal cord of the sea lamprey. J. Physiol. (London) 212: 65–83.

Martin, A. R., W. O. Wickelgren, and R. Beránek. 1970. Effects of iontophoretically applied drugs on spinal interneurones of the lamprey. J. Physiol. (London) 207: 653–665.

Martin, R. J. 1978. Glycine and GABA receptors on lamprey bulbar reticulospinal neurones. Comp. Biochem. Physiol. C, 61: 37–40.

1979. A study of the morphology of the large reticulospinal neurons of the lamprey ammocoete by intracellular injection of Procion yellow. Brain Behav. Evol. 16: 1–18.

Martin, R. J., and D. Bowsher. 1977. An electrophysiological investigation of the projection of the intramedullary primary afferent cells of the lamprey ammocoete. Neurosci. Lett. 5: 39–43.

Matthews, G., and W. O. Wickelgren. 1977. Effects of guanidine on transmitter release and neuronal excitability. J. Physiol. (London) 266: 69–89.

1978a. Trigeminal sensory neurons of the sea lamprey. J. Comp. Physiol. A, 123: 329–333.

1978b. Sustained depolarizing potentials in reticulospinal axons during evoked seizure activity in lamprey spinal cord. J. Neurophysiol. 41: 384–393.

1978c. Evoked depolarizing and hyperpolarizing potentials in reticulospinal axons of lamprey. J. Physiol. (London) 279: 551–567.

1979a. Glycine, GABA and synaptic inhibition of reticulospinal neurones of lamprey. J. Physiol. (London). 293: 393–415.

1979b. Glutamate and synaptic excitation of reticulospinal neurones of lamprey. J. Physiol. (London) 293: 417–433.

Meyer, W. 1979. Oxidative enzymes and myosin–ATPase in the trunk musculature of the river lamprey (*Lampetra fluviatilis*). Histochem. J. 11: 187–195.

Müller, H. 1968. Feinstruktur und Lipidbildung der Fettzellen im Perimeningealgewebe von Neunaugen unter normalen and experimentallen Bedingungen. Z. Zellforsch. Mikrosk. Anat. 84: 585–608.

Nakao, T. 1976a. An electron microscopic study of the neuromuscular junction in the myotomes of larval lamprey, *Lampetra japonica*. J. Comp. Neurol. 165: 1–15.

Nakao, T. 1976b. Electron microscopic studies on the myotomes of larval lamprey, *Lampetra japonica*. Anat. Rec. 187: 383–403.

1979. Electron microscopic studies on the lamprey meninges. J. Comp. Neurol. 183: 429–453.

Niazi, I. A. 1963. The histology of tail regeneration of the ammocoetes. Can. J. Zool. 41: 125–146.

Nieuwenhuys, R. 1967. Comparative anatomy of olfactory centres and tracts. Progr. Brain Res. 23: 1–64.

1977. The brain of the lamprey in a comparative perspective. Ann. N.Y. Acad. Sci. 299: 97–145.

Northcutt, R. G. 1979a. Experimental determination of the primary trigeminal projections in lampreys. Brain Res. 163: 323–327.

1979b. Central projections of the eighth cranial nerve in lampreys. Brain Res. 167: 163–167.

Ochi, J., and Y. Hosoya. 1974. Fluorescence microscopic differentiation of monoamines in the hypothalamus and spinal cord of the lamprey, using a new filter system. Histochemistry 40: 263–266.

Ogorodnikova, L. G., and E. B. Fomina. 1977. Glucose-6-phosphatase activity in the pia mater of certain vertebrates. J. Evol. Biochem. Physiol. (Transl.) 13: 201–204.

Öhman, P. 1971. The photoreceptor outer segments of the river lamprey (*Lampetra fluviatilis*). An electron-, fluorescence- and light microscopic study. Acta Zool. (Stockholm) 52: 287–297.

1974. Fine structure of the retinal pigment epithelium of the river lamprey (*Lampetra fluviatilis*, Cyclostomi). Acta Zool. (Stockholm) 55: 245–253.

1976. Fine structure of photoreceptors and associated neurons of *Lampetra fluviatilis* (Cyclostomi). Vision Res. 16: 659–662.

1977. Fine structure of the optic nerve of *Lampetra fluviatilis* (Cyclostomi). Vision Res. 17: 719–722.

Peters, A., and B. MacKay. 1961. The structure and innervation of the myotomes of the lamprey. J. Anat. 95: 575–585.

Petrovický, P. 1977. Formatio reticularis and nucleus motorius tegmenti in the lamprey (*Lampetra fluv.*) a comparative study. Acta Univ. Carol. Med. 23: 203–220.

Pfenninger, K. H., and C. M. Rovainen. 1974. Stimulation- and calcium-dependence of vesicle attachment sites in the presynaptic membrane; a freeze-cleave study on the lamprey spinal cord. Brain Res. 72: 1–23.

Pfister, C. 1971a. Die Matrixentwicklung in Tel- und Diencephalon von *Lampetra planeri* (Bloch) (Cyclostomata) in Verlaufe des Individualzyklus. J. Hirnforsch. 13: 363–375.

1971b. Die Matrixentwicklung in Mes- und Rhombencephalon von *Lampetra planeri* (Bloch) (Cyclostomata) im Verlaufe des Individualzyklus. J. Hirnforschung 13: 377–383.

Plisetskaya, E. M. 1967. Respiration and glycogen content in lamprey brain, p. 149–155. *In* Evolutionary neurophysiology and neurochemistry. Nauka, Leningrad. (In Russian)

1968. Brain and heart glycogen content in some vertebrates and the effect of insulin. Endocrinol. Exp. 2: 251–262.

Poon, M. L. T. 1980. Induction of swimming in lamprey by L-DOPA and amino acids. J. Comp. Physiol. A, 136: 337–344.

Potter, I. C., B. J. Hill, and S. Gentleman. 1970. Survival and behaviour of ammocoetes at low oxygen tensions. J. Exp. Biol. 53: 59–73.

Pu, G. A., and J. E. Dowling. 1980. Physiological properties of the pineal photoreceptor in the larval lamprey, *Petromyzon marinus*. In preparation.

Randall, D. J. 1972. Respiration, p. 287–306. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2. Academic Press, London.

Ringham, G. L. 1975. Localization and electrical characteristics of a giant synapse in the spinal cord of the lamprey. J. Physiol. (London) 251: 395–407.

Roberts, A., and B. P. Hayes. 1977. The anatomy and function of "free" nerve endings in an amphibian skin sensory system. Proc. R. Soc. Ser. B, 196: 415–429.

Roberts, T. D. M. 1950. The respiratory movements of the lamprey (*Lampetra fluviatilis*). Proc R. Soc. Edinburgh, Sect. B, 64: 235–252.

Rovainen, C. M. 1967a. Physiological and anatomical studies on large neurons of central nervous system of the sea lamprey (*Petromyzon marinus*). I. Müller and Mauthner cells. J. Neurophysiol. 30: 1000–1023.

1967b. Physiological and anatomical studies on large neurons of central nervous system of the sea lamprey (*Petromyzon marinus*). II. Dorsal cells and giant interneurons. J. Neurophysiol. 30: 1024–1042.

1970. Glucose production by lamprey meninges. Science 167: 889–890.

1974a. Synaptic interactions of identified nerve cells in the spinal cord of the sea lamprey. J. Comp. Neurol. 154: 189–206.

1974b. Synaptic interactions of reticulospinal neurons and nerve cells in the spinal cord of the sea lamprey. J. Comp. Neurol. 154: 207–223.

1974c. Respiratory motoneurons in lampreys. J. Comp. Physiol. 94: 57–68.

1976a. Regeneration of Müller and Mauthner axons after spinal transection in larval lampreys. J. Comp. Neurol. 168: 545–554.

1976b. Vestibulo-ocular reflexes in the adult sea lamprey. J. Comp. Physiol. A, 112: 159–164.

1977. Neural control of ventilation in the lamprey. Fed. Proc. Fed. Am. Soc. Exp. Biol. 36: 2386–2389.

1978. Müller cells, "Mauthner" cells and other identified reticulospinal neurons in the lamprey, p. 245–269. *In* D. S. Faber and H. Korn [ed.] Neurobiology of the Mauthner cell. Raven Press, NY.

1979a. Electrophysiology of vestibulospinal and vestibulo-reticulospinal systems in lampreys. J. Neurophysiol. 42: 745–766.

1979b. Neurobiology of lampreys. Physiol. Rev. 59: 1007–1077.

Rovainen, C. M., and K. L. Birnberger. 1971. Identification and properties of motoneurons to fin muscle of the sea lamprey. J. Neurophysiol. 34: 974–982.

Rovainen, C. M., P. A. Johnson, E. A. Roach, and J. A. Mankovsky. 1973. Projections of individual axons in lamprey spinal cord determined by tracings through serial sections. J. Comp. Neurol. 149: 193–201.

Rovainen, C. M., G. E. Lemcoe, and A. Peterson. 1971. Structure and chemistry of glucose-producing cells in meningeal tissue of the lamprey. Brain Res. 30: 99–118.

Rovainen, C. M., O. H. Lowry, and J. V. Passonneau. 1969. Levels of metabolites and production of glucose in the lamprey brain. J. Neurochem. 16: 1451–1458.

Rovainen, C. M., and M. H. Schieber. 1975. Ventilation of larval lampreys. J. Comp. Physiol. 104: 185–203.

Rubinson, K. 1974. The central distribution of VIII nerve afferents in larval *Petromyzon marinus*. Brain Behav. Evol. 10: 121–129.

Rubinson, K., and M. C. Kennedy. 1979. The organization of the optic tectum in larval, transforming, and adult sea lamprey, *Petromyzon marinus*. Proceedings of the NATO Advanced Study Institute, Developmental Neurobiology of Vision, Crete, Greece, 1978.

Rubinson, K., H. Ripps, P. Witkovsky, and M. C. Kennedy. 1977. Retinal development in the lamprey, *Petromyzon marinus*. Soc. Neurosci. Abstr. 3: 575.

Saito, T. 1930. Über das Gehirn des japanischen Flussneunauges (*Entosphenus japonicus* Martens). Folia Anat. Jap. 8: 189–263.

Sakharov, D. A., and L. A. Kashapova. 1979. The primitive pattern of the vertebrate body muscle innervation: ultrastructural evidence for two synaptic transmitters. Comp. Biochem. Physiol. A, 62: 771–776.

Sawyer, P. J. 1959. Burrowing activities of the larval lamprey. Copeia 1959: 256–257.

Schober, W. 1964. Vergleichend-anatomische Untersuchungen am Gehirn der Larven und adulten Tiere von Lampetra fluviatilis (Linné, 1758) und Lampetra planeri (Bloch, 1784). J. Hirnsforsch. 7: 107–209.

Schultz, R., E. C. Berkowitz, and D. C. Pease. 1956. The electron microscopy of the lamprey spinal cord. J. Morphol. 98: 251–273.

Schwab, M. E. 1973. Some new aspects about the prosencephalon of *Lampetra fluviatilis* (L.). A cytoarchitectural and comparative study. Acta Anat. 86: 353–375.

Selzer, M. E. 1978a. Mechanisms of functional recovery and regeneration after spinal cord transection in larval sea lamprey. J. Physiol. (London) 277: 395–408.

1978b. The action of phenytoin on a composite electrical–chemical synapse in the lamprey spinal cord. Ann. Neurol. 3: 202–206.

1979a. Variability in maps of identified neurons in the sea lamprey spinal cord examined by a wholemount technique. Brain Res. 163: 181–193.

1979b. The effect of phenytoin on the action potential of a vertebrate spinal neuron. Brain Res. 171: 511–521.

Shapovalov, A. I. 1977. Interneuronal synapses with electrical and chemical modes of transmission and evolution of the central nervous system. J. Evol. Biochem. Physiol. (Transl.) 13: 434–444.

Smith, D. S. 1971. On the significance of cross-bridges between microtubules and synaptic vesicles. Phil. Trans. R. Soc. London, Ser. B, 261: 395–405.

Smith, D. S., U. Järlfors, and R. Beránek. 1970. The organization of synaptic axoplasm in the lamprey (*Petromyzon marinus*) central nervous system. J. Cell Biol. 46: 199–219.

Stefanelli, A. 1934. I centri tegmentali dell'encefalo die petromizonti. Arch. Zool. Ital. 20: 117–202.

1937. Il sistema statico dei Petromizonti (sistema laterale, sistema vestibolare, cervelletto). I: Centri nervosi e vie centrali. Arch. Zool. Ital. 24: 209–273.

Stefanelli, A., and S. Caravita. 1970. Ultrastructural features of the synaptic complex of the vestibular nuclei of *Lampetra planeri* (Bloch). Z. Zellforsch. Mikrosk. Anat. 108: 282–296.

Stent, G. S., W. B. Kristan Jr., W. O. Friesen, C. A. Ort, M. Poon, and R. L. Calabrese. 1978. Neuronal generation of the leech swimming movement. Science 200: 1348–1357.

Sterba, G., G. Hoheisel, R. Wegelin, W. Naumann, and F. Schober. 1979. Peptide containing vesicles within neuro-neuronal synapses. Brain Res. 169: 55–64.

Sterzi, G. 1907. Il Nervosa Centrale Dei Vertebrati. Vol. 1. Ciclostomi. Draghi, Padova. p. 29–514.

Suzuki, N. 1974. Intracellular responses of lamprey olfactory receptors to current and chemical stimulation, p. 13–22. *In* Y. Katsuki, M. Sato, S. F. Takagi, and Y. Oomura [ed.] Food intake and chemical senses. University of Tokyo Press, Tokyo.

1978. Effects of different ionic environments on the responses of single olfactory receptors in the lamprey. Comp. Biochem. Physiol. A, 61: 461–467.

Tamarova, Z. A. 1978. Electrotonic excitatory postsynaptic potentials induced by stimulating the ventral roots in motor neurons and Müller axons of the lamprey, *Lampetra fluviatilis*. J. Evol. Biochem. Physiol. (Transl.) 14: 486–492.

Tang, D., and M. E. Selzer. 1979. Projections of lamprey spinal neurons determined by the retrograde axonal transport of horseradish peroxidase. J. Comp. Neurol. 188: 629–645.

Tavolga, W. N. 1971. Sound production and detection, p. 135–205. *In* W. S. Hoar and D. J. Randall [ed.] Fish Physiology. Vol. 5. Academic Press, NY.

Teeter, J. H. 1980. Pheromone communication in sea lampreys (*Petromyzon marinus*): implications for population management. Can. J. Fish. Aquat. Sci. 37: 2123–2132.

Teräväinen, H. 1971. Anatomical and physiological studies on muscles of lamprey. J. Neurophysiol. 34: 954–973.

Teräväinen, H., and C. M. Rovainen. 1971a. Fast and slow motoneurons to body muscle of the sea lamprey. J. Neurophysiol. 34: 990–998.

1971b. Electrical activity of myotomal muscle fibers, motoneurons, and sensory dorsal cells during spinal reflexes in lampreys. J. Neurophysiol. 34: 999–1009.

Thornhill, R. A. 1970. Cell division in the olfactory epithelium of the lamprey, *Lampetra fluviatilis*. Z. Zellforsch. Mikrosk. Anat. 109: 147–157.

1972. The development of the labyrinth of the lamprey (*Lampetra fluviatilis*), Linn. 1758). Proc. R. Soc. Ser. B, 181: 175–198.

Tretjakoff, D. 1909a. Das Nervensystem von Ammocoetes I. Das Rückenmark. Arch. Mikrosk. Anat. Entwicklungsmech. 73: 607–680.

1909b. Das Nervensystem von Ammocoetes II. Gehirn. Arch. Mikrosk. Anat. Entwicklungsmech. 74: 636–779.

1927a. Das periphere Nervensystem des Flussneunauges. Z. Wiss. Zool. 129: 359–452.

1927b. Die Fettglycogenzellen beim Neunauge. Anat. Anz. 63: 72–82.

Veselkin, N. P. 1966. Electrical reactions in midbrain, medulla and spinal cord of lamprey to visual stimulation. Fed. Proc. Trans. Suppl. 25: 957–960.

Wächtler, K. 1974. The distribution of acetylcholinesterase in the cyclostome brain: I. *Lampetra planeri* (L.) Cell Tissue Res. 152: 259–270.

1978. The regional distribution of cholinacetyl transferase and acetylcholinesterase in the brain of the lamprey (*Petromyzon fluviatilis*). Comp. Biochem. Physiol. C, 61: 411–413.

Wallén, P. 1977. On the spinal generation of locomotion in fish. *In* Neurophysiological mechanisms of locomotion. 27th Int. Cong. of Physiol. Sat. Symp., Paris.

Walls, G. L. 1963. The vertebrate eye and its adaptive radiation. Hafner, New York. p. 555–562.

Whiting, H. P. 1957. Mauthner neurons in young larval lampreys (*Lampetra* spp.). Q. J. Microsc. Sci. 98: 163–178.

Wickelgren, W. O. 1977a. Physiological and anatomical characteristics of reticulospinal neurones in lamprey. J. Physiol. (London) 270: 89–114.

1977b. Post-tetanic potentiation, habituation and facilitation of synaptic potentials in reticulospinal neurones of lamprey. J. Physiol. (London) 270: 115–131.

Wood, M. R., and M. J. Cohen. 1979. Synaptic regeneration in identified neurons of the lamprey spinal cord. Science 206: 344–347.

Woodburne, R. T. 1936. A phylogenetic consideration of the primary and secondary centers and connections of the trigeminal complex in a series of vertebrates. J. Comp. Neurol. 65: 403–501.

Yamada, Y. 1973. Fine structure of the ordinary lateral line organ: I. The neuromast of lamprey, *Entosphenus japonicus*. J. Ultrastruct. Res. 43: 1–17.

Osmoregulation in Juvenile and Adult Lampreys[1]

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Beamish, F. W. H. 1980. Osmoregulation in juvenile and adult lampreys. Can. J. Fish. Aquat. Sci. 37: 1739–1750.

Nonparasitic lampreys are well adapted for a freshwater existence but are less tolerant of salt water than representatives of the parasitic species. Anadromous feeding juvenile sea lampreys, *Petromyzon marinus*, are able to control serum osmotic and ionic concentrations in all salinities between 0 and 34‰. Juveniles of the anadromous European river lamprey, *Lampetra fluviatilis*, are slightly less tolerant of salinity change. The transition of *P. marinus* to a landlocked existence has resulted in a reduction in the capacity for marine osmoregulation. Tolerance to salt water among landlocked *P. marinus* is related directly to size emphasizing the advantage afforded through a reduction of surface area relative to body volume. Changes in serum osmolality are primarily the result of corresponding shifts in sodium and chloride ions. Changes in chloride are not accompanied by an equivalent shift in sodium suggesting that the relationship between the two ions is not passive. Regulation of sodium by landlocked *P. marinus* is not precise as that exhibited by the anadromous form particularly in the higher salinities. Nontrophic upstream migrant lampreys display a reduction in their marine osmoregulatory mechanisms and a restoration of the freshwater osmoregulatory apparatus. Freshwater osmotic and ionic regulation deteriorates in spent adult lampreys.

Key words: blood, ionic regulation, osmotic regulation, parasitic and nonparasitic lampreys, salinity, life cycle

Beamish, F. W. H. 1980. Osmoregulation in juvenile and adult lampreys. Can. J. Fish. Aquat. Sci. 37: 1739–1750.

Les lamproies non parasites sont bien adaptées à une existence en eau douce mais sont moins tolérantes à l'eau salée que les représentants d'espèces parasites. Les jeunes lamproies marines, *Petromyzon marinus*, anadromes et se nourrissant peuvent régler les concentrations osmotiques et ioniques de leur sérum à toute salinité entre 0 et 34‰. Les jeunes de la lamproie fluviatile européenne anadrome, *Lampetra fluviatilis*, sont légèrement moins tolérants à un changement de salinité. Le passage de *P. marinus* à une existence confinée en eau douce entraîna une diminution de capacité osmorégulatrice en mer. Chez *P. marinus* confiné en eau douce, la tolérance à l'eau salée est directement liée à la taille, ce qui fait ressortir l'avantage d'une diminution de surface par rapport au volume du corps. Les changements d'oxmolalité sérique résultent avant tout du glissement correspondant des ions sodium et chlorure. Les changements de chlorure ne sont pas accompagnés d'un glissement équivalent de sodium, suggérant que la relation entre les deux ions n'est pas passive. La régulation du sodium par *P. marinus* confiné en eau douce n'est pas aussi précise que celle de la forme anadrome, en particulier aux fortes salinités. Les lamproies se déplaçant vers l'amont montrent une diminution de leurs mécanismes d'osmorégulation en mer et une restauration de leur appareil osmorégulateur d'eau douce. La régulation osmotique et ionique d'eau douce se détériore chez les lamproies adultes qui ont frayé.

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Most vertebrates are tolerant of small changes in internal ionic composition and concentration. However, the variation compatible with life is extremely limited. Among marine teleosts and cyclostomes (Petromyzontia) body water is lost from the hypoosmotic blood at the gills and across the integument (Black 1957). Water loss is countered by a low urine production (Morris 1972), swallowing of seawater (Krogh 1939), and the entrance of ambient water across the integument (Potts 1968). Cyclostomes, unlike teleosts, have no mineralized tissue with which to exchange and accumulate ions of the extracellular fluid and blood (Urist 1963). Excess monovalent ions absorbed from the digestive tract are believed to be secreted by specialized gill epithelial or "chloride" cells in both the cyclostomes and teleosts (Keys 1931; Doyle and Gorecki 1961; Threadgold and Houston 1964; Picker-

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ing and Morris 1976). Divalent ions remain in the gut and are removed in the feces (Hoar 1966). Freshwater homeostasis depends on the elimination of water from the hyperosmotic blood coupled with the transportation of ions from the ambient environment or, in the case of teleosts, from skeletal stores. The osmotic influx of water in freshwater fishes is controlled by a copious dilute urine (Parry 1966; Morris 1972). Salt loss is replaced from ingested food (Hoar 1966) and active recruitment by the ion-transporting or "chloride" cells (Peek and Youson 1979a).

Juvenile lampreys are found in both fresh and saline waters. Those species which do not feed during the juvenile interval of their life cycle are found only in freshwater. Of the parasitic species some spend the juvenile trophic portion of their life cycle in saline water before returning as adults to freshwater rivers in which they reproduce and thereafter die. Other parasitic species remain in freshwater throughout their entire life cycle. This report summarizes present information on the capacity of juvenile and adult lampreys for ionic and osmotic regulation and the mechanisms by which control is achieved.

Regulatory Mechanisms

Water balance and ionic-composition and concentration are regulated in lampreys by the gills, kidney, gut, and integument. In a saline environment juvenile lampreys maintain water and ion balance by drinking seawater. Monovalent ions are absorbed by specialized cells located in the anterior portion of the digestive tract, with any excess being excreted via the gills. Most divalent ions remain in the gut and are excreted along with the nondigestible components of the ingested food. Excess divalent ions which enter the body fluids are excreted by the kidneys in concentrated urine. In juvenile lampreys the foregut is a new structure which develops during transformation by formation of a lumen in a solid epithelial chord (Hardisty et al. 1970). The timing of the opening of the foregut appears not to be in synchrony within and among species, a factor which would be expected to contribute to variability in osmoregulatory efficiency. Thus, while the foregut of most specimens of the anadromous *Lampetra fluviatilis* opens by late October, it may remain closed in some animals until May (Weissenberg 1927). Presumably the foregut opens earlier in *Petromyzon marinus* than in river lampreys (Hardisty and Potter 1971). In freshwater, ion balance is maintained by the active uptake of salts at the gills, gut, and kidney together with the production of dilute urine.

The gills of many teleosts and lampreys are characterized by specialized ion transport cells widely known as "chloride" cells. In the marine or estuarine environment, chloride cells are believed to be involved in ion excretion whereas in freshwater they are thought to be responsible for ion absorption. Chloride cells are involved also in the elimination of nitrogenous wastes in the form of ammonia (Read 1968; De Renzis and Maetz 1973; Evans 1975) which may account at least in part for their active appearance in lampreys adapted to freshwater (Peek and Youson 1979a). Several types of chloride cells are present within the gill epithelium of most fishes (Doyle and Gorecki 1961; Threadgold and Houston 1964) and the anadromous *P. marinus* (Peek and Youson 1979a), likely reflecting stages of cell differentiation (Conte and Lin 1967) or cells at various levels of activity (Shirai and Utida 1970). The appearance of cells is influenced also by the ambient salinity (Philpott and Copeland 1963; Shirai and Utida 1970).

Ultrastructural studies on the interlamellar regions of juvenile and adult lamprey gills (Nakao 1974, 1977; Pickering and Morris 1976; Youson and Freeman 1976; Peek and Youson 1979a) suggest the presence of chloride cells with similar features to those displayed by marine teleosts (Philpott and Copeland 1963; Shirai and Utida 1970; Newstead 1971; Kikuchi (1977). Chloride cells from lampreys have abundant mitochondria and a highly developed reticulum of smooth cytoplasmic tubules continuous with the lateral and basal plasma membranes. The continuity of the smooth endoplasmic reticulum with the plasma membrane in young juvenile landlocked *P. marinus* (Youson and Freeman 1976) has been observed also in the chloride cells of *L. japonica* (Nakao 1974; Nakao and Uchinomiya 1974) and early upstream migrants of *L. fluviatilis* (Morris and Pickering 1976).

Among larval lampreys, chloride cells are few in number and resemble those identified in freshwater teleosts in that their smooth endoplasmic reticulum is confined to the apical cytoplasm in the form of vesicles. Chloride cells in larval lampreys are rich in mitochondria (Morris and Pickering 1975; Youson and Freeman 1976) and are believed to assist in ion uptake. The rapid increases in osmolality which have been observed for landlocked sea lamprey during metamorphosis (Mathers and Beamish 1974) appear to coincide with the early formation of the juvenile type of chloride cell (Peek and Youson 1979b). During the upstream spawning migration the juvenile type of chloride cells degenerate and are replaced by the larval type (Morris and Pickering 1976).

The biochemical mechanism by which lampreys transport ions across the gill epithelium has only recently been studied (Beamish et al. 1978). At the site of the chloride cells a sodium–potassium dependent ATPase enzyme ((Na–K)-ATPase) has been identified in both teleosts (Epstein et al. 1967; Kamiya and Utida 1968; Pfeiler and Kirschner 1972; Zaugg and McLain 1976) and anadromous sea lampreys (Beamish et al. 1978). This enzyme is believed to constitute the pump responsible for the outward transport of sodium and inward movement of potassium across the gill epithelium (Adams et al. 1975). Gill (Na–K)-ATPase activity is absent in ammocoetes of the anadromous sea lamprey but present in young feeding juveniles of this species (Beamish et al. 1978). Peek and Youson (1979a) suggest that the site of (Na–K)-ATPase may be the membrane of the cytoplasmic tubules in the chloride cells.

Gill (Na–K)-ATPase activity declines with the age of the anadromous sea lamprey, being highest in young feeding animals in salt water and effectively absent from spawning migrants in freshwater. The functioning of (Na–K)-ATPase in small juvenile sea lampreys presumably enhances the efficiency with which they are able to make the transition from fresh to salt water. Once lampreys begin feeding, the composition of body fluids ingested from the host fish may facilitate osmoregulation and at the same time stimulate the animal's capacity for osmoregulation making the role of the enzyme less important. Further, as lampreys increase in size the corresponding reduction of the surface area in relation to volume lowers the osmotic stress exerted by the external medium.

Lamprey kidneys are largely responsible for excreting osmotic water and the absorption of solutes which in freshwater assists in the preservation of the ionic composition of body fluids (Morris 1960). The paired kidneys are usually unequal in size, with one longer and of greater cross-sectional area (Youson et al. 1974). The structure of the larval pronephros and opisthonephros has been described in detail (Wheeler 1899; Hatta 1900; Inukai 1929; Youson and McMillan 1970a, b, 1971a, b). The larval kidney degenerates anteriorly throughout life and disappears entirely during metamorphosis at which time the opisthonephros develops (Schneider 1879; Youson 1970; Ooi and Youson 1979). The opisthonephric kidney degenerates gradually until the end of the spawning migration when a massive deterioration occurs (Morris 1972). Details of the structure of the opisthonephros are given in Muller (1875), Meyer (1876), Wheeler (1899), Krause (1921), Vinnichenko (1966), Youson and McMillan 1970a, b, 1971a, b), and others.

Measurements of urine production and quality have been made for lampreys in freshwater (Wikgren 1953; Sawyer 1955; Morris 1956; Hardisty 1956; Bentley 1962; Bentley and Follett 1963; Bull and Morris 1967; Pickering and Morris 1970; Malvin et al. 1970). Most measurements are, however, subject to question due to handling diuresis (Morris 1972) or the effects of anesthesia (Moriarty et al. 1978). The most reliable measurements indicate that lampreys have a high urine production relative to that of freshwater teleosts. Some ions are excreted in association with the high production of urine. Wikgren (1953) estimated electrolyte excretion in the urine to represent 2.5–30% of the total ionic loss. Other estimates have been made and are discussed in detail in Morris (1972). Calculations by Morris (1972) for lampreys in freshwater suggest that sodium, potassium, and chloride are largely reabsorbed by the kidney although absorption efficiency for potassium is not high. Further, the kidney reabsorbs approximately one half of the water produced as a result of glomerular filtration (Morris 1972). Efficiency of ion absorption and water reabsorption varies directly with temperature (Wikgren 1953). Morris (1972) suggests that this is consistent with the hypothesis that water absorption is a passive process resulting from the osmotic flow of water from the urine to the blood. Thus, a reduction in ion absorption at low temperature could cause a decline in water reabsorption.

Permeability of the integument to water has been investigated for *L. planeri* and *L. fluviatilis* in freshwater by ligating the urinogenital papilla and measuring weight change (Hardisty 1956). Urine production determined in this manner coincided percisely with direct measurements made by Wikgren (1953). Hardisty (1956) suggests that the branchial epithelium plays the major role in water transport. On the basis of equal body weights the permeability of the integument to water was estimated to be about twice as great in *L. planeri* as in *L. fluviatilis.*

In salt water, juvenile lampreys are believed to produce very limited quantities of urine (Morris 1972). It is important to point out that kidney function in salt water is poorly understood for lampreys. On the basis of glomerular filtration rates obtained by Bentley and Follett (1963) together with consideration for tubular absorption of water, Pickering and Morris (1970) calculated that kidney tubules preferentially secrete divalent ions.

Regulation of salt and water balance in the higher vertebrates is under hormonal control. Water excretion among the higher vertebrates may be regulated by one or more hypophysial peptides such as arginine vasotocin (Robertson 1974). Among the primitive cyclostomes the physiological importance of hypophysial peptides is still uncertain (Hardisty 1972; Robertson 1974). Injection of arginine vasotocin into *L. fluviatilis* did not cause a change in body weight nor urine volume. It did, however, cause an elevation in urine sodium and potassium with an increased total renal loss of sodium (Bentley and Follett 1963). Presumptive adrenocortical cells exist in association with the cardinal veins of lampreys and may be the source of corticosteroids influencing salt and water balance (Chester Jones 1963). An attempt to identify and quantify cortisol and corticosterone in the plasma of the landlocked sea lamprey has shown only doubtful traces of these compounds (Weisbart and Idler 1970). Injections of aldosterone caused a slight decline in urine output but significant changes in total urinary loss of sodium or potassium were not demonstrable (Bentley and Follett 1963). In saline water aldosterone reduced the total loss of sodium which caused Bentley and Follett (1963) to suggest that the hormone inhibits the extrarenal loss of sodium at the gills. Certainly, at present it is not possible to generalize on the hormones present in the pituitary–hypothalamus complex or those of the adrenocortical tissue, or on their function in osmotic and ionic regulation (Robertson 1974; Larsen 1980; Gorbman 1980).

Regulation and Salinity Tolerance During Metamorphosis

Subsequent to the freshwater sedentary larval stage, lampreys undergo a nontrophic period of metamorphosis during which a number of morphological and physiological changes occur (Manion and Stauffer 1970; Hardisty and Potter 1971; Potter et al. 1978). Among the parasitic lampreys, these changes include the machinery by which internal ionic and osmotic concentration can be regulated over a greater range of ambient salinities than can be tolerated by the larvae. Ammocoetes are well adapted for life in freshwater; however, in saline water they exhibit a rather ineffective control of their internal osmotic and ionic concentration (Hardisty 1956; Morris 1972; Mathers and Beamish 1974; Beamish et al. 1978). Accordingly larval lampreys have a relatively low tolerance for salt water. Mortalities of larval anadromous sea lamprey were recorded in a salinity as low as 10‰ with the 24-h LC50 being 14.8‰ (Beamish et al. 1978). Larvae of the nonparasitic species appear equally sensitive to salinity. Thus, Hardisty (1956) found mortalities among larval *L. planeri* in solutions of NaCl equivalent to about 280 mosmol $\cdot$ kg^{-1} or 11‰.

Osmotic regulation during metamorphosis has been measured only for the landlocked sea lamprey (Mathers and Beamish 1974). During the early stages of metamorphosis serum osmolality of the landlocked sea lamprey in freshwater increases rapidly reaching a plateau by the early macrophthalmia stage (Fig. 1, Mathers and Beamish 1974). Serum osmolality of larval sea lampreys in freshwater is ~260 mosmol $\cdot$ kg^{-1}. By the early macrophthalmia stage osmolality increases to 304 mosmol $\cdot$ kg^{-1} and remains at a similar level to the completion of metamorphosis. Not until the macrophthalmia stage is reached are sea lampreys able to osmoregulate in a saline solution equivalent to 10‰. After 1 d exposure to a salinity of 10‰, osmolality of ammocoetes and metamorphosing stages III and IV (Manion and Stauffer 1970) are ~344, 333, and 335 mosmol $\cdot$ kg^{-1}, respectively. Osmolality of early macrophthalmia in 10‰ is about 300 mosmol $\cdot$ kg^{-1}, similar to that in freshwater.

Salinity Tolerance in Juveniles and Adults

On completion of metamorphosis, parasitic juvenile lampreys migrate downstream to either a lake or ocean where they begin the second trophic interval of their life cycle. Completion of the downstream migration may be delayed by as much as 6 mo during which time lampreys remain within the river without feeding (Applegate 1950; Potter and Beamish 1977). Of those species which spend their juvenile interval in freshwater only the landlocked *P. marinus* has been examined with respect to salinity tolerance and osmotic performance (Mathers and Beamish 1974). Among the marine lampreys, osmotic relationships have been determined for *P. marinus*, *L. fluviatilis*, and *Lampetra tridentata* (Fontaine 1930; Galloway 1933; Hardisty 1956; Morris 1956, 1958; Pickering and Morris 1970; Potter and Huggins 1973; Beamish et al. 1978; J. Richards, Dep. Fish. Oceans, Nanaimo, B.C., personal communication).

Adjustment to seawater soon after metamorphosis has been demonstrated for *P. marinus* (Beamish et al. 1978), *L. fluviatilis* (Hardisty 1956; Potter and Huggins 1973), and *L. tridentata* (J. Richards personal communication). Direct transfer of young anadromous juvenile *P. marinus* and *L. tridentata* to full seawater did not result in any mortalities within a 2-wk experimental period. Indeed, the transfer of *L. tridentata* to full seawater appears to encourage the initiation of feeding. Young juvenile *L. fluviatilis* are slightly better able to withstand direct transfer from fresh to full seawater than metamorphosing individuals of the same species (Potter and Huggins 1973). However, for both stages some mortalities were recorded over the 3-wk experimental period. Mortality of downstream migrant individuals captured in March was 25‰ when exposed to full seawater compared with 20‰ among animals taken in May/early June. About 30% of the metamorphosing animals when transferred directly to full seawater died within the experimental 3-wk period. Survival of juveniles was almost complete if the transfer to full seawater was made by exposing animals to increments of one third seawater each for 4 d.

Tolerance to salt water among the landlocked *P. marinus* is related to size of the feeding animals (Mathers and Beamish 1974). Over one half of the landlocked feeding juveniles of 127–188 mm died within 10 d following direct transfer to 26‰. Only when landlocked juveniles reached almost 280 mm did they survive direct transfer to full seawater for periods of ~2 wk.

Coincident with the completion of the juvenile interval and the migration into freshwater rivers prior to reproduction is a marked reduction in the marine osmoregulatory mechanism. Galloway (1933) and (1956) found that adult migrant anadromous *P. marinus* and *L. fluviatilis* immersed in one half seawater died within 24 h. Beamish et al. (1978) determined the salinity at which 50% of the anadromous early upstream migrant *P. marinus* died within 48 h to be ~15.2‰ which is in general accord with that found by Morris (1956).

Nonparasitic lampreys appear to be less tolerant of salinity than representatives of the parasitic species. Hardisty (1956) found some mortalities among juvenile *L. planeri* exposed to a solution of 10‰ NaCl. Mortality was complete at 22 and 34‰ NaCl within 6 and 3 h, respectively. More recently J. Richards (personal communication) found that gradual exposure of juvenile *L. richardsoni* to saline water equivalent to 15‰ resulted in total mortality within 4 or 5 d.

Osmotic and Ionic Regulation

The regulatory mechanisms in marine feeding lam-

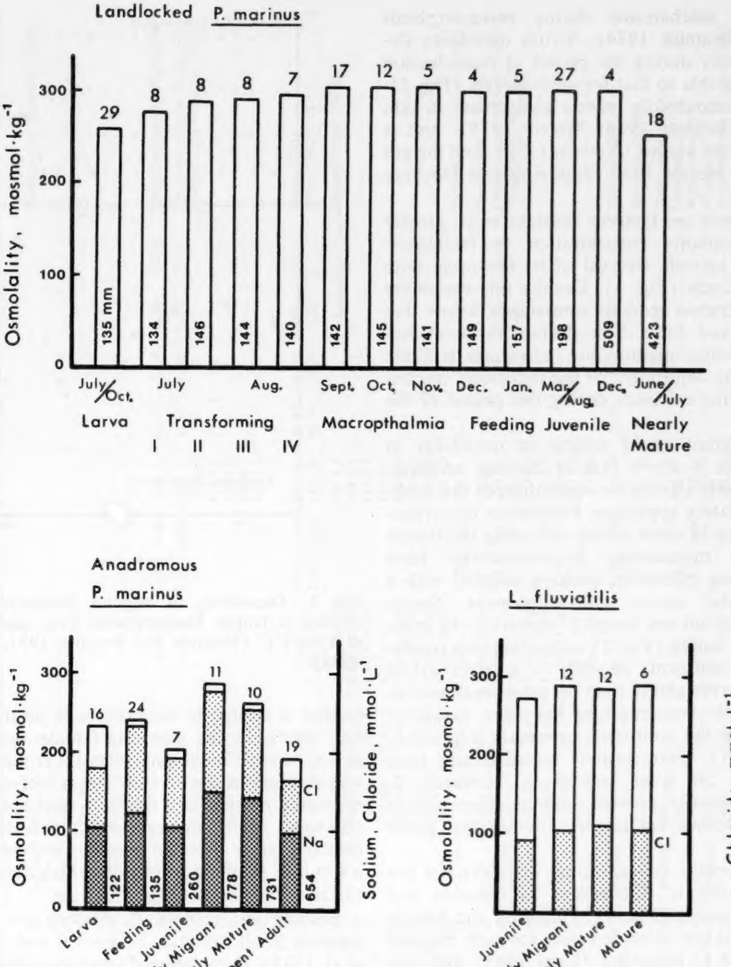

FIG. 1. Osmolality, chloride, and sodium concentration of the life stages of the landlocked and anadromous *Petromyzon marinus* (Mathers and Beamish 1974; Beamish et al. 1978) and *Lampetra fluviatilis* (Dekhuyzen 1904; Galloway 1933; Hardisty 1956; Pickering and Morris 1970) in freshwater. Values for *P. marinus* (10 ± 1°C) are based on blood serum, those for *L. fluviatilis* on plasma. Mean length (mm) is given within or beside the bar and the sample size is provided on top of each bar.

preys are well developed but unable to provide for complete blood homoiosmoticity between fresh and full seawater. Juveniles of the landlocked forms and the nonparasitic species are unable to maintain as tight a control over their blood concentration in saline water as that exhibited by the anadromous species. Feeding individuals of all species that are tolerant of the saline environment maintain their blood hyperosmotic to freshwater and hypoosmotic to seawater.

In freshwater, feeding landlocked sea lampreys exhibit osmotic independence (Urist and Van der Putte 1967; Mathers and Beamish 1974). There is, however, a significant increase in osmotic concentration between the larval and juvenile stage which signals a change in the regulatory mechanisms during metamorphosis (Mathers and Beamish 1974). Serum osmolality declines precipitously during the period of reproduction to a level comparable to that for ammocoetes (Fig. 1). This decrease undoubtedly reflects an increase in skin permeability (Hardisty 1956; Morris 1958), and a degeneration of the kidney (Youson 1970), and the gut (Pickering and Morris 1970; Pickering and Dockray 1972).

The anadromous sea lamprey displays much greater variability in osmotic concentration in freshwater throughout the juvenile interval of its life cycle than the landlocked form (Fig. 1). Despite this variability osmotic concentration remains consistently below that for the landlocked form. The decline in osmolality with size of feeding anadromous individuals is likely a reflection of the adjustment of the regulatory mechanisms for a marine existence during this period of the life cycle.

Upstream migrant adults exhibit an osmolality in freshwater which is above that of feeding juveniles. This rise apparently signals the restoration of the freshwater osmoregulatory apparatus. Freshwater osmoregulation deteriorates in spent adults indicating the tissues responsible for maintaining hyperosmoticity have ceased functioning efficiently, perhaps coupled with a leakage of water across the integument. Serum osmolality in migrant sea lamprey appears to be independent of body length (Fig. 2) suggesting that regulation of ionic constituents depends to a lesser extent on integument permeability than on other mechanisms.

Plasma osmotic concentration has been measured in freshwater for the nontrophic upstream migrant *L. fluviatilis* (Fig. 1). Unfortunately measurements have not been made on spent individuals. However, *L. fluviatilis* demonstrates greater osmotic independence than the anadromous sea lamprey during this phase of the life cycle.

Changes in osmotic concentration in freshwater are mainly attributable to fluctuations in chloride and sodium concentrations (Fig. 1). Pickering and Morris (1970) suggest the low chloride values for early migrant *L. fluviatilis*, and *L. tridentata* (Urist 1963) indicates that the freshwater regulatory mechanism is incompletely established when individuals first enter freshwater. However, in the anadromous sea lampreys both sodium and chloride were higher in early migrants than in feeding animals and decreased with the approach of sexual maturity.

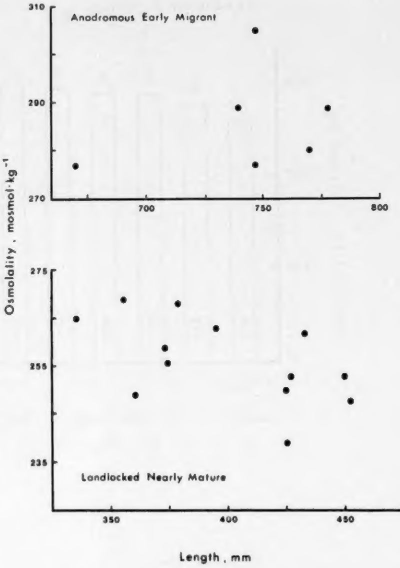

FIG. 2. Osmolality of migrant *Petromyzon marinus* in relation to length. Measurements were made in freshwater at 10 ± 1°C (Mathers and Beamish 1974; Beamish et al. 1978).

Relatively few measurements have been made of other blood ions (Table 1). Consistent and low levels of serum calcium and phosphate are prevalent in the blood of the landlocked sea lamprey (Urist and Van der Putte 1967). Urist (1963) has shown that the lamprey is a typical freshwater vertebrate in its serum calcium and phosphate levels. About 28 and 11% of calcium and phosphate is present as a complex with protein. Early migrant female lampreys display higher calcium levels than males which Pickering and Dockray (1972) suggest is related to the process of producing calcium-rich vitellin by the maturing female. Serum potassium in a normally functioning animal is regulated by sodium and throughout the juvenile stages of feeding and early migration remains at a similar concentration. In mature and spent adult lampreys potassium levels are approximately double those in juvenile individuals, probably a result of leaching from cells which deteriorate during this terminal period of the life cycle.

Feeding anadromous *P. marinus* are able to osmoregulate in all salinities between 0 and 34‰ (Beamish et al. 1978). Osmolality of small juveniles of ~138 mm in length remains essentially unchanged at 236 mosmol·kg^{-1} between 0 and 16‰ (Table 1, Fig. 3). In higher salinities osmolality increases but only by 10% in full seawater. Small juveniles are capable of acclimating to daily increments of 2‰ exhibiting no significant change in osmolality over exposure periods of 1–8 d following a given increase in salinity. Serum osmolality of large feeding juveniles, ~282 mm in length increases continuously between 0 and 26‰, the highest salinity in which the species has been examined (Fig. 3). However, for identical salinities significant differences in osmolality between the two size-classes of feeding individuals are demonstrable only in freshwater. Both size-classes maintained hyperosmotic blood serum in 0 and 8‰ and hypoosmotic in higher salinities.

Small feeding juvenile landlocked sea lampreys main-

TABLE 1. Blood plasma or serum osmotic and ionic concentrations.

Species		Stage	Salinity %	Serum/ plasma	Osmolality mOs·kg⁻¹	Na^+	K^-	Ca^{++}	Mg^{++}	Cl^-	SO_4^{--}	HCO^{3-}	P^{--}	Protein mg·mL⁻¹	Reference
						mmol·L⁻¹									
P. marinus (landlocked)		Metamorphosing													
		Stage I	0	Serum	277 ± 5[a]										Mathers and Beamish (1974)
		Stage II	0	"	288 ± 10										" " " "
		Stage III	0	"	290 ± 5										" " " "
		Stage IV	0	"	297 ± 3										" " " "
		Macrophthalmia	0	"	304 ± 6										" " " "
		Stage III	10	"	333 ± 11										" " " "
		Stage IV	10	"	335 ± 6										" " " "
		Macrophthalmia	10	"	301 ± 5										" " " "
		Metamorphosing	0	"		134	4.00	2.40	1.80	122	0.10	5.00	1.30	32.0	Urist and van der Putte (1967)
	Juvenile	Feeding	0	Serum		137	3.30	2.20	2.00	122	0.10	5.00	1.40	35.0	Urist and van der Putte (1967)
		"	0	"	300 ± 2	141 ± 1				121 ± 2					Mathers and Beamish (1974)
		"	0	"	292 ± 10	136 ± 3				118 ± 4					" " " "
		"	16	"	323 ± 12	149 ± 3				136 ± 2					" " " "
		"	26	"	352 ± 10	164 ± 4				145 ± 6					" " " "
		"	32	"	398 ± 17	186 ± 7				173 ± 10					" " " "
	Adult	Migrant	0	"	257 ± 6										" " " "
		Migrant	0	"		139	6.20	2.37	1.90	113	0.87	5.18	1.40	39.0	Urist (1963)
		Spawning	0	"		136	5.10	2.47	1.75	112	0.74	5.21	1.31		Urist (1963)
P. marinus (anadromous)	Juvenile	Feeding (small)	0	Serum	238 ± 7	117 ± 4	7.45 ± 0.82[b]			109 ± 5					Beamish et al. (1978)
		" "	8	"	236 ± 9	114 ± 5	6.08 ± 0.44[b]			118 ± 7					" "
		" "	16	"	234 ± 5	106 ± 5	4.42 ± 0.37[b]			121 ± 3					" "
		" "	26	"	256 ± 4	115 ± 7	4.37 ± 0.33[b]			123 ± 3					" "
		" "	34	"	263 ± 3	135 ± 3	5.39 ± 0.42[b]			126 ± 4					" "
		Feeding (large)	0	"	203 ± 16	93 ± 7	3.49 ± 1.33[b]			87 ± 5					" "
		Feeding (large)	8	"	214 ± 26	95 ± 12	6.39 ± 2.00[b]			95 ± 14					" "
		Feeding (large)	26	"	250	126 ± 3	5.63 ± 2.77[b]			124 ± 2					" "
		Feeding	35	"[c]		155 ±	31.6	3.51	6.99	158	4.4				Robertson, in Morris (1972)
	Adult	Early migrant	0	"	285 ± 9	155 ± 5	4.95 ± 1.11[b]			125 ± 5					Beamish et al. (1978)
		Early migrant	0	Plasma	294	112	2.3	1.8	1.5	100			2.5		Pickering and Morris (1970)
		Early migrant	0	Plasma	319					119			1.8		Fontaine (1930, 1932)
		Nearly mature	0	Serum	259 ± 8	136 ± 7	5.57 ± 1.82[b]			112 ± 5					Beamish et al. (1978)
		" "	8	"	250 ± 8	128 ± 5	4.01 ± 1.25[b]			119 ± 10					" "
		" "	16	"	358 ± 30	175 ± 16	4.98 ± 1.09[b]			168 ± 14					" "
		" "	24	"	460 ± 69	223 ± 29	10.85 ± 7.72[b]			217 ± 76					" "
		Spent	0	"	190 ± 10	92 ± 7	11.03 ± 2.05[b]			67 ± 6					" "
L. tridentata	Adult	Early migrant	0	Serum		87	6.12	2.80	1.40	80	0.50	3.12	4.71		Urist (1963)
L. planeri	Adult		0	Serum	227					101					Hardisty (1956)
L. fluviatilis	Adult		0	Plasma	280										Dekhuyzen (1904)
			0		265			1.32		92					Galloway (1833)
			0			115	3.1	0.95	1.00	92					Robertson (1954)
		Early migrant	0	Plasma	288					112					Hardisty (1956)
			0		260	120				95					Pickering and Morris (1970)
		Nearly mature	0	Plasma	274					118					Hardisty (1956)
			0		297	122				107					Pickering and Morris (1970)
		Mature	0	Plasma	289	122				106					Pickering and Morris (1970)

[a] Confidence limits 95%.
[b] Beamish (unpublished data).
[c] High values due to some hemolysis of the sample.

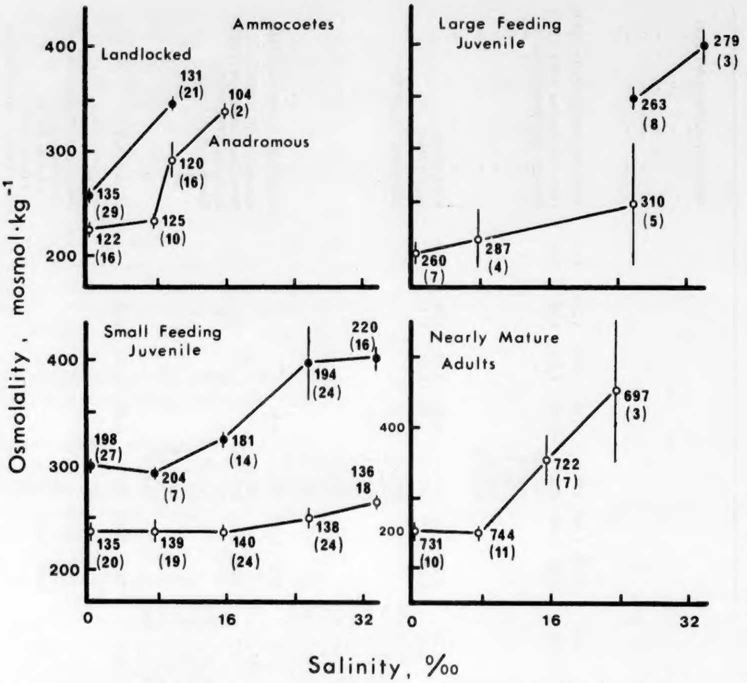

FIG. 3. Serum osmolality of the life stages of the anadromous and landlocked sea lamprey in relation to salinity. Vertical bars around the mean denote 95% confidence limits. The mean body length (mm) and sample size, in parentheses, is indicated for each osmolality.

tain higher serum osmolalities than the anadromous form when compared at identical salinities (Beamish et al. 1978). The landlocked form is unable to maintain as tight a control over serum osmolality in saline water as that displayed by the anadromous form (Mathers and Beamish 1974; Beamish et al. 1978, Fig. 3). Only the large feeding landlocked sea lampreys are able to osmoregulate for long periods in salinities above 16‰. Within 10 d in 26‰ over 50% of the juvenile lampreys (127–188 mm) died. Osmolality of lampreys (194 mm) surviving for 10 d (397 mosmol·kg^{-1}) was considerably above that of individuals (203 mm) after 1 d in 26‰ (354 mosmol·kg^{-1}). Osmotic concentration of the larger sea lampreys did not change significantly during the 15-d exposure period. The landlocked form of sea lamprey (220 mm) in 34‰ was able to maintain serum osmolality (401 mosmol·kg^{-1}) constant for 4 d. By the 9th d in 34‰ all animals died. Similarly lampreys of 250 mm did not survive longer than 9 d in 34‰. The largest category of lampreys tested, 289 mm, survived the 15 d in 34‰ without mortality. Further, osmotic concentration did not vary appreciably from 400 mosmol·kg^{-1} throughout the exposure period. Concordant with the lower serum osmolalities recorded for the anadromous form of *P. marinus*, Burian (1910) found the osmotic concentration for one feeding animal captured in the Mediterranean Sea, 42‰, to be 317 mosmol·kg^{-1}, well below that for the landlocked form in a salinity of 34‰ and above that recorded for anadromous feeding juveniles by Beamish et al. (1978). More recently, Robertson (in Morris 1972) reported an osmolality of ~360 mosmol·kg^{-1} for a sea lamprey caught off the coast of Scotland in a salinity of 35‰.

Serum osmolality in freshwater relative to ambient salinity for the landlocked and anadromous forms of *P. marinus* were compared by Beamish et al. (1978). The ratio for landlocked juveniles decreased from 1.00 to 0.76 between 0 and 26‰ whereas that for the anadromous individuals declined only to 0.93 over the same salinity range. It appears that with the transition to a landlocked existence lampreys have experienced a reduction in their capacity for marine osmoregulation. The large landlocked juveniles are able to osmoregulate even in full seawater emphasizing the advantage afforded through a reduction of surface area relative to body volume.

Changes in serum osmolality appear to be primarily

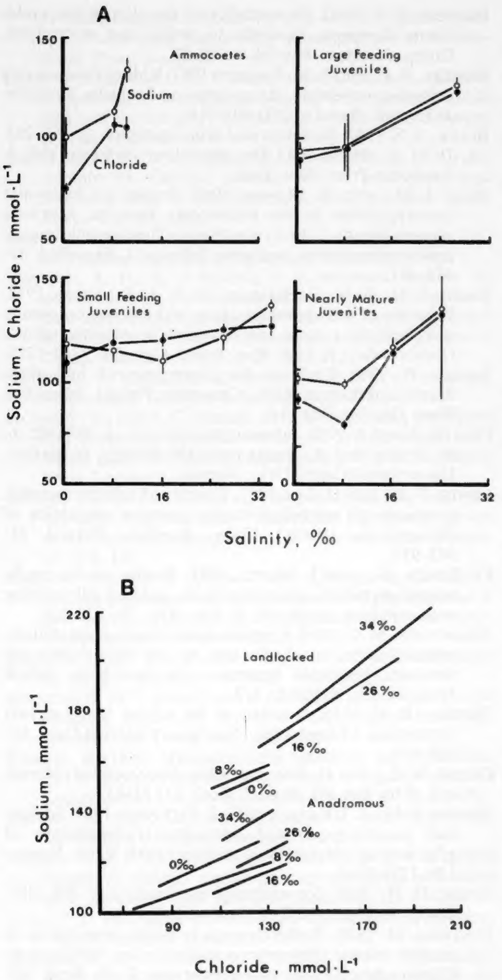

FIG. 4(A). Serum sodium and chloride concentrations of the anadromous sea lamprey. Vertical bars around the mean denote 95% confidence limits. (B) Relationship of serum sodium to chloride concentrations. Redrawn from Beamish et al. (1978).

the result of corresponding shifts in sodium and chloride ions (Table 1, Fig. 4A) (Urist and van der Putte 1967; Mathers and Beamish 1974; Beamish et al. 1978). Organic molecules such as glucose, glycerol, and amino acids along with some inorganic ions account for the difference between osmolality and sodium plus chloride (Potts and Parry 1964). In both landlocked and anadromous feeding sea lampreys, changes in chloride ion are not accompanied by an equivalent shift in sodium, suggesting that the relationship between the two ions is not passive (Fig. 4B). For a given change in chloride, that by sodium was less; however, this was not as pronounced in the higher salinities (Fig. 4A). The close control held over sodium has been demonstrated also for several teleosts (Houston et al. 1968; Byrne et al. 1972; Lutz 1972). Lutz (1972) suggests that the physiological significance of sodium is in the uptake of metabolites by the cell as well as in the regulation of potassium. Landlocked *P. marinus* are not able to regulate sodium as precisely as anadromous sea lampreys, particularly in the higher salinities, which may contribute to the difficulties they experience in salt water.

Early migrants of the anadromous *L. fluviatilis* fail to regulate their internal osmotic concentration in salinities above ~18‰ (Hardisty 1956). Between freshwater and the isosmotic salinity the hyperosmotic blood serum increases from a value between ~250 and 300 (Dekhuyzen 1904; Galloway 1933; Hardisty 1956; Pickering and Morris 1970) to 450 mosmol·kg^{-1} (Hardisty 1956), well above the range of concentrations found for the feeding stages of both the anadromous and landlocked forms of *P. marinus* (Mathers and Beamish 1974; Beamish et al. 1978).

Osmoregulatory performance among the nonparasitic lampreys has been examined in relation to ambient salinity only for *L. planeri* (Hardisty 1956). Animals maintain a hyperosmotic blood serum to a salinity of about 12‰ at which regulation of the internal concentration ceases and some mortalities occur.

Nearly mature migrant anadromous sea lampreys are able to regulate their osmotic concentration in dilute saline solutions to about 8‰ (Beamish et al. 1978). Exposure of nearly mature sea lampreys to 8‰ for 4 d did not alter significantly the osmolality found after 1 d in this salinity. In 16‰ serum osmolality rose precipitously to 358 mosmol·kg^{-1}, a significant increase over that found at the lower salinities. The increase in osmolality continued to 24‰ at which it was 460 mosmol·kg^{-1}. Loss of the swallowing mechanism and a reduced capacity to absorb ions and water across the gut wall were suggested by Pickering and Morris (1970) as factors contributing to the breakdown of the marine osmoregulatory ability in upstream migrating sea lampreys and *L. fluviatilis*. Freshwater osmoregulation deteriorated in spent adults. Osmolality and the concentration of sodium and chloride dropped below those of any other stage in freshwater indicating that the tissues responsible for maintaining hyperosmoticity had ceased to function efficiently, perhaps coupled with a leakage of ions or water across the integument. An increase in integument permeability to water was reported by Morris (1958) and Pickering and Morris (1970) in *L. fluviatilis* and *P. marinus* on the spawning migration. Hardisty (1956) found increased body water in *L. planeri* and *L. fluviatilis* as each approached sexual maturity. Regulation is restricted further by a massive degeneration of the kidneys which occurs at the time of spawning (Youson 1970).

The habitat of the earliest agnathans is uncertain. Robertson (1954, 1957) has argued in favor of a marine environment on the basis of paleontological and physiological evidence, the former being supported more recently by the findings of Denison (1956), White (1958), and Tarlo (1962). In contrast, Marshall and Smith (1930) proposed a freshwater origin and based their views on the presence of a glomerular kidney. Robertson (1957) and Morris (1965, 1972) have suggested the vertebrate glomerulus may have developed in seawater where it served primarily as an organ of ion balance. In support of this, Youson et al. (1974) were unable to detect significant differences in the cross-sectional area of the renal corpuscles of freshwater and marine sea lampreys. Certainly a glomerular kidney would have facilitated the entry of cyclostomes into freshwater. Volume regulation and conservation of ions by the production of a hypoosmotic urine together with the function of ion regulation would permit animals to maintain a hyperosmotic blood in an ion-deficient environment (Robertson 1957, 1974; Munz and McFarland 1964). On balance, Morris (1972) concluded the earliest agnathans were marine animals equipped with a primitive osmoregulatory mechanism similar to that of the present-day myxinoids. He suggests that cyclostomes more recently entered freshwater and adapted their metabolic processes to function in a concentration of blood ions below that which is prevalent in marine forms, thereby reducing the osmotic stress between the internal and external environment. The subsequent reentry into the marine habitat may have been facilitated by the development of a swallowing extrarenal excretory mechanism.

The present-day landlocked forms of parasitic lampreys as well as the nonparasitic species are believed to have evolved from marine parasitic species (Hubbs 1925, Hubbs and Potter 1971). Hardisty (1956) suggested that this evolution involved selection for individuals of smaller size and reduced osmoregulatory performance which is entirely consistent with recent observations on salinity tolerance, and osmotic and ionic regulation.

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Adams, B. L., W. S. Zaugg, and L. R. McLain. 1975. Inhibition of salt water survival and Na-K ATPase elevation in steelhead trout (*Salmo gairdneri*) by moderate water temperatures. Trans. Am. Fish. Soc. 104: 766–769.

Applegate, V. C. 1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. Serv. 55: 237.

Beamish, F. W. H., P. D. Strachan, and E. Thomas. 1978. Osmotic and ionic performance of the anadromous sea lamprey, *Petromyzon marinus*. Comp. Biochem. Physiol. 60A: 435–443.

Bentley, P. F. 1962. Permeability of the skin of the cyclostome *Lampetra fluviatilis* to water and electrolytes. Comp. Biochem. Physiol. 6: 95–97.

Bentley, P. J., and B. K. Follett. 1963. Kidney function in a primative vertebrate, the cyclostome *Lampetra fluviatilis*. J. Physiol. (Lond.), 169: 902–918.

Black, V. S. 1957. Excretion and osmoregulation, p. 163–205. *In* M. E. Brown [ed.] The physiology of fishes. Vol. 1. Academic Press, New York.

Bull, J. M., and R. Morris. 1967. Studies on freshwater osmoregulation in the ammocoete larva or *Lampetra planeri* (Bloch). I. Ionic constituents fluid compartments, ionic compartments and water balance. J. Exp. Biol. 47: 485–494.

Byrne, J. M., F. W. H. Beamish, and R. L. Saunders. 1972. Influence of salinity temperature, and exercise on plasma osmolarity and ionic concentration in Atlantic salmon (*Salmo salar*). J. Fish. Res. Board Can. 29: 1217–1220.

Burian, R. 1910. Funktion der nierenglomeruli und ultrafiltration, Pfluegers Arch. Gesamten Physiol. Menschen Tiere 136: 741–760.

Chester Jones, I. 1963. Adrenocorticosteroids, p. 488–502. *In* A. Brodal and R. Fange [ed.] The biology of myxine. Universitetsforlaget, Oslo, Norway.

Conte, F. P., and D. Lin. 1967. Kinetics of cellular morphogenesis in gill epithelium during seawater adaptation of *Oncorhynchus* (Walb.). Comp. Biochem. Physiol. 23: 945–957.

De Renzis, G., and J. Maetz. 1973. Studies on the mechanisms of chloride absorption by the goldfish gill: relation with acid-base regulation. J. Exp. Biol. 59: 339–358.

Dekhuyzen, M. C. 1904. Ergebnisse von osmotischen studien, namentlich bei knochenfischen, an der biologischen station des bergenser museums. Bergens Mus. Arbok Naturvitensk. Rekke 8: 3–7.

Denison, R. H. 1956. A review of the habitat of the earliest vertebrates. Chicago Nat. Hist. Mus. Fieldiana Geol. 11: 359–457.

Doyle, W. L., and D. Gorecki. 1961. The so-called chloride cell of the fish gill. Physiol. Zool. 34: 81–85.

Epstein, F. H., A. I. Katz, and G. E. Pickford. 1967. Sodium and potassium-activated adenosine triphosphatase of gills: role in adaptation of teleosts to salt water. Science 156: 1245–1247.

Evans, D. H. 1975. Ion exchange mechanisms in fish gills. Comp. Biochem. Physiol. 51A: 491–495.

Fontaine, M. 1930. Recherches sur le milieu interieur de la lamproi marine (*Petromyzon marinus*). Ses variations en fonction de celles du milieu exterieur. C. R. Acad. Sci. Paris 191: 680–682.

1932. Sur la relation existant chez les poissons marins et potamotoques entre le teneur en phosphore inorganique du serum et l'ossification du squellete. C. R. Acad. Sci. Paris 194: 395–396.

Galloway, T. McL. 1933. The osmotic pressure and saline content of the blood of *Petromyzon fluviatilis*. J. Exp. Biol. 10: 313–316.

Gorbman, A. 1980. Evolution of the brain-pituitary relationship: evidence from the Agnatha. Can. J. Fish. Aquat. Sci. 37: 1680–1686.

Hardisty, M. W. 1956. Some aspects of osmotic regulation in lampreys. J. Exp. Biol. 33: 431–447.

1972. The interrenal, p. 171–192. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London.

Hardisty, M. W., and I. C. Potter. 1971. The general biology of adult lampreys, p. 126–207. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London.

Hardisty, M. W., I. C. Potter, and R. Sturge. 1970. A comparison of the metamorphosing and macrophthalmia stages of the lampreys *Lampetra fluviatilis* and *L. planeri*. J. Zool. 162: 383–400.

Hatta, S. 1900. Contributions to the morphology of Cyclostomata. II. On the development of pronephros and segmental duct in Petromyzon. J. Coll. Sci. Imp. Univ. Tokyo 13: 311–426.

Hoar, W. S. 1966. General and comparative physiology. 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, NJ. 848 p.

Houston, A. H., R. S. Reaves, J. A. Madden, and M. A. de Wilde. 1968. Environmental temperature and the body fluid system of the freshwater teleost. I. Ionic regulation in thermally acclimated rainbow trout (*Salmo gairdneri*). Comp. Biochem. Physiol. 25: 563–582.

Hubbs, C. L. 1925. The life cycle and growth of lampreys. Mich. Acad. Sci. Arts Lett. Pap. 4: 587–603.

Hubbs, C. L., and I. C. Potter. 1971. Distribution, phylogeny and taxonomy, p. 1–65. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London.

Inukai, T. 1929. Die Vorniere (Pronephros) auf ihrer hochsten Entwick lungsstufe bei Neunaugen (*Lampetra* (*Petromyzon*) *fluviatilis* und *planeri*). Z. Mikrosk. Anat. Forsch. 19: 139–162.

Kamiya, M., and S. Utida. 1968. Changes in activity of sodium–potassium activated adenosine triphosphatase in gills during adaptation of the Japanese eel to sea water. Comp. Biochem. Physiol. 26: 675–685.

Keys, A. 1931. Chloride and water secretion and absorption by the gills of the eel. Z. Vergl. Physiol. 15: 364.

Kikuchi, S. 1977. Mitochondria-rich (chloride) cells in the gill epithelia from four species of stenohaline freshwater teleosts. Cell Tissue Res. 180: 87–98.

Krause, R. 1921. Mikroskopische anatomie der wirbeltiere, p. 746–858. *In* Teleostier, Plagiostomen, Zyklostomen und Leptokardier. Vol. 4. Walter De Gruyter & Co., Berlin.

Krogh, A. 1939. Osmotic regulation in aquatic animals. Cambridge University Press, NY. 242 p.

Larsen, L. O. 1980. Physiology of adult lampreys with special regard to natural starvation, reproduction, and death after spawning. Can. J. Fish. Aquat. Sci. 37: 1762–1779.

Lutz, P. L. 1972. Ionic patterns in the teleost. Comp. Biochem. Physiol. 42(3A): 719–733.

Malvin, R. L., E. Carlson, S. Legan, and P. Churchill. 1970. Creatinine reabsorption and renal function in the freshwater lamprey. Am. J. Physiol. 218: 1506–1509.

Manion, P. J., and T. M. Stauffer. 1970. Metamorphosis of the landlocked sea lamprey, *Petromyzon marinus*. J. Fish. Res. Board Can. 27: 1735–1746.

Marshall, E. K., and H. W. Smith. 1930. The glomerular development of the vertebrate kidney. Biol. Bull. Mar. Biol. Lab. (Woods Hole, Mass.) 59: 135–153.

Mathers, J. S., and F. W. H. Beamish. 1974. Changes in serum osmotic and ionic concentration in landlocked *Petromyzon marinus*. Comp. Biochem. Physiol. 49A: 677–688.

Meyer, F. 1876. Ueber due Nieren der Flussneunaugen, *Petromyzon fluviatilis*. Ztrbl. Med. Wiss. 14: 20–21.

Muller, W. 1875. Ueber das Urinogenitalysystem des Amphioxus und der cyclostomen. Jena. Z. Naturwiss. 9: 94–129.

Moriarty, R. J., A. G. Logan, and J. C. Rankin. 1978. Measurement of single nephron filtration rate in the kidney of the river lamprey, *Lampetra fluviatilis* L. J. Exp. Biol. 77: 57–69.

Morris, R. 1956. The osmoregulatory ability of the lampern (*Lampetra fluviatilis* L.) in sea water during the course of its spawning migration. J. Exp. Biol. 33: 235–248.

1958. The mechanism of marine osmoregulation in the lampern (*Lampetra fluviatilis* L.) and the causes of its breakdown during the spawning migration. J. Exp. Biol. 35: 649–665.

1960. General problems of osmoregulation with special reference to cyclostomes. Symp. Zool. Soc. London 1: 1–16.

1965. Studies on salt and water balance in *Myxine glutinosa* (L.). J. Exp. Biol. 42: 359–371.

1972. Osmoregulation, p. 193–239. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2. Academic Press, London.

Morris, R., and A. D. Pickering. 1975. Ultrastructure of the presumed ion-transporting cells in the gills of ammocoete lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch.). Cell Tissue Res. 163: 327–341.

1976. Changes in the ultrastructure of the gills of the river lamprey, *Lampetra fluviatilis* (L.), during the anadromous spawning migration. Cell Tissue Res. 173: 271–277.

Munz, F. W., and W. N. McFarland. 1964. Regulatory function of a primative vertebrate kidney. Comp. Biochem. Physiol. 13: 381–400.

Nakao, T. 1974. Fine structure of the agranular cytoplasmic tubules in the lamprey chloride cells. Anat. Rec. 178: 49–62.

1977. Electron microscopic studies of coated membranes in two types of gill epithelial cells of lampreys. Cell Tissue Res. 178: 385–396.

Nakao, T., and K. Uchinomiya. 1974. Intracisternal tubules of lamprey chloride cells. J. Electronmicrosc. 23: 51–55.

Newstead, J. D. 1971. Observations on the relationship between "chloride-type" and "pseudobranch-type" cells in the gills of a fish, *Oligocottus maculosus*. Z. Zellforsch. Mikrosk. Anat. 116: 1–6.

Ooi, E. C., and J. H. Youson. 1979. Regression of the larval opisthonephros during metamorphosis of the sea lamprey, *Petromyzon marinus* L. Am. J. Anat. 154: 57–79.

Parry, G. 1966. Osmotic adaptation in fishes. Biol. Rev. Cambridge Philos. Soc. 41: 392–444.

Peek, W. D., and J. H. Youson. 1979a. Ultrastructure of chloride cells in young adults of the anadromous sea lamprey, *Petromyzon marinus* L., in fresh water and during adaptation to sea water. J. Morphol. 160: 143–164.

1979b. Transformation of the interlamellar epithelium of the gills of the anadromous sea lamprey, *Petromyzon marinus* L., during metamorphosis. Can. J. Zool. 57: 1318–1332.

Pfeiler, E., and L. B. Kirschner. 1972. Studies on gill ATPase of rainbow trout (*Salmo gairdneri*). Biochim. Biophys. Acta 282: 301–310.

Philpott, C. W., and D. E. Copeland. 1963. Fine structure of chloride cells from three species of *Fundulus*. J. Cell Biol. 18: 389–404.

Pickering, A. D., and G. J. Dockray. 1972. The effects of gonadectomy on osmoregulation in the migrating river lamprey, *Lampetra fluviatilis* L. Comp. Biochem. Physiol. 41A: 139–147.

Pickering, A. D., and R. Morris. 1970. Osmoregulation of

Lampetra fluviatilis and *Petromyzon marinus* in hypertonic solutions. J. Exp. Biol. 53: 231–243.

1976. Fine structure of the interplatelet area in the gills of the macrophthalmia stage of the river lamprey, *Lampetra fluviatilis* (L.) Cell Tissue Res. 168: 433–443.

Potter, I. C., and F. W. H. Beamish. 1977. The freshwater biology of adult anadromous sea lampreys *Petromyzon marinus*. J. Zool. (London) 181: 113–130.

Potter, I. C., and R. J. Huggins. 1973. Observations on the morphology, behaviour and salinity tolerance of downstream migrating river lampreys (*Lampetra fluviatilis*). J. Zool. (London) 169: 365–379.

Potter, I. C., G. M. Wright, and J. H. Youson. 1978. Metamorphosis of anadromous sea lamprey, *Petromyzon marinus* L. Can. J. Zool. 56: 561–570.

Potts, W. T. W. 1968. Osmotic and ionic regulation. Annu. Rev. Physiol. 30: 73–104.

Potts, W. T. W., and G. Parry. 1964. Osmotic and ionic regulation in animals. Pergamon Press Ltd., Oxford. 423 p.

Read, L. J. 1968. A study of ammonia and urea production and excretion in the freshwater-adapted form of the Pacific lamprey *Entosphenus tridentatus*. Comp. Biochem. Physiol. 26: 455–466.

Robertson, J. D. 1954. The chemical composition of the blood of some aquatic chordates, including members of the Tunicata, Cyclostomata and Osteichthyes. J. Exp. Biol. 31: 424–442.

1957. The habitat of the early vertebrates. Biol. Rev. 32: 156–187.

1974. Osmotic and ionic regulation in cyclostomes, p. 169–193. *In* M. Florkin and B. T. Scheer [ed.] Chemical zoology. Vol. VIII: Primitive Deuterostomians, Cyclostomata, Fishes. Academic Press, New York.

Sawyer, W. H. 1955. Excretion and osmoregulation. *In* M. E. Brown [ed.] The physiology of fishes. Vol. 1. Academic Press, New York. 194 p. (Unpublished data from V. S. Black)

Schneider, A. 1879. Beitrage zur vergleichenden Anatomie und Entwicklung-sgeschichte der Wirbelthiere. Reimer, Berlin. p. 85–92.

Shirai, N., and S. Utida. 1970. Development and degeneration of the chloride cells during seawater and freshwater adaptation of the Japanese eel, *Anguilla japonica*. Z. Zellforsch. 103: 247–264.

Tarlo, L. B. 1962. The classification and evolution of the Heterostraci. Acta Palaeontol. Polon. 8: 249–290.

Threadgold, L. T., and A. H. Houston. 1964. An electron microscope study of the "chloride cell" of *Salmo salar* L Exp. Cell Res. 34: 1–23.

Urist, M. R. 1963. The regulation of calcium and other ions in the serums of hagfish and lampreys. Ann. N.Y. Acad. Sci. 109: 294–311.

Urist, M. R., and K. A. van de Putte. 1967. Comparative biochemistry of the blood of fishes: identification of fishes by the chemical composition of serum, p. 271–285. *In* P. W. Gilbert, R. F. Mathewson, and D. P. Rall [ed.] Sharks, skates and rays. John Hopkins Press, Baltimore.

Vinnichenko, L. N. 1966. Electron microscope studies of lamprey kidney. *In* Elekromaya Mikroskopiya Kletov Zhwotnych. Nauka, Moscow.

Weisbart, M., and D. R. Idler. 1970. Re-examination of the presence of corticosteroids in two cyclostomes, the Atlantic hagfish (*Myxine glutinosa* L.) and the sea lamprey (*Petromyzon marinus* L.). J. Endocrinol. 46: 29–43.

Weissenberg, R. 1927. Beitrage zur Kenntnis der Biologie und Morphologie der Neunaugen. 2. Das Refewachstum der Gonaden bei *Lampetra fluviatilis* und *planeri*. Z. Mikrosk. Anat. Forsch. 8: 193–249.

Wheeler, W. M. 1899. The development of the urinogenital organs of the lamprey. Zool. Jahrb. Abt. Anat. Ontog. Tiere 73: 7–88

White, E. I. 1958. Original environment in Craniates, p. 212–234. *In* T. S. Westoll [ed.] Studies on fossil vertebrates. Academic Press, London.

Wikgren, B. J. 1953. Osmotic regulation in some aquatic animals with special reference to the influence of temperature. Acta Zool. Fenn. 71: 1–102.

Youson, J H. 1970. Observations on the opisthonephric kidney of the sea lamprey of the Great Lakes, *Petromyzon marinus* L., at various stages during the life cycle. Can. J. Zool. 48: 1313–1316.

Youson, J. H., and P. A. Freeman. 1976. Morphology of the gills of larval and parasitic adult sea lamprey, *Petromyzon marinus* L. J. Morphol. 149: 73–104.

Youson, J. H., S. J. Hansen, and I. M. Campbell. 1974. A quantitative comparison of the kidneys of the landlocked sea lamprey of the Great Lakes and the anadromous sea lamprey of the Atlantic, *Petromyzon marinus* L. Can. J. Zool. 52: 1447–1455.

Youson, J. H., and D. B. McMillan. 1970a. The opisthonephric kidney of the sea lamprey of the Great Lakes. Part 1. The renal corpuscle. Am. J. Anat. 127: 207–232.

1970b. The opisthonephric kidney of the sea lamprey of the Great Lakes. Part 2. Neck and proximal segments of the tubular nephron. Am. J. Anat. 127: 233–257.

1971a. The opisthonephric kidney of the sea lamprey of the Great Lakes. Part 3. Intermediate, distal and collecting segments of the adult. Am. J. Anat. 130: 281–303.

1971b. The opisthonephric kidney of the sea lamprey of the Great Lakes. Part 4. Intermediate, distal and collecting segments of the adult. Am. J. Anat. 130: 281–303.

Zaugg, W. S., and L. R. McLain. 1976. Influence of water temperature on gill sodium, potassium-stimulated ATPase activity in juvenile coho salmon (*Oncorhynchus kisutch*). Comp. Biochem. Physiol. 54A: 419–421.

Biology and Physiology of Feeding in Adult Lampreys[1]

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FARMER, G. J. 1980. Biology and physiology of feeding in adult lampreys. Can. J. Fish. Aquat. Sci. 37: 1751–1761.

Although landlocked sea lampreys (*Petromyzon marinus*) attack all but a few of the smallest teleosts in the Great Lakes, the large cold-water species have received the most predation. Information on the feeding habits of anadromous lampreys is limited, but they probably are not specific in their choice of hosts. Species differences exist in the relative proportions of blood and muscle tissue which are consumed. The landlocked sea lamprey primarily feeds on the blood of host fishes at rates of 3–30% of its wet body weight·d^{-1} (10°C). The estimated gross conversion efficiency for this species feeding ad libitum at 10°C is 39%. This relatively high efficiency is partly attributable to the nature of their blood diet which results in small fecal energy losses of about 3.4% of intake energy. Maximum growth rates occur at 20°C for sea lampreys of 10–30 g initial weight and at 15°C for lampreys of 30–90 g. At all experimental temperatures (5–20°C), growth rates decline with increases in lamprey weight. Increases in sea lamprey weight and in water temperature up to 20°C cause the rate of host mortality to rise suggesting that, under natura lconditions, mortality is seasonal. Landlocked sea lampreys show a preference for specific areas on their hosts, select larger hosts more frequently, and are not attracted to hosts that have lampreys feeding on them. Such strategies serve to maximize food intake and prolong host survival while ensuring food material of constant energy content.

Key words: adult lampreys, feeding, hosts, growth rate, temperature, host mortality, behavior

FARMER, G. J. 1980. Biology and physiology of feeding in adult lampreys. Can. J. Fish. Aquat. Sci. 37: 1751–1761.

Bien que la grande lamproie marine (*Petromyzon marinus*) confinée en eau douce attaque tous les téléostéens, sauf les plus petits, dans les Grands Lacs, ce sont les grandes espèces d'eau froide qui ont souffert le plus de la prédation. Nos connaissances du comportement alimentaire des lamproies anadromes sont limitées, mais ces dernières ne choisissent probablement pas un hôte particulier. Il y a des différences spécifiques de proportions relatives de sang et de tissu musculaire consommés. La lamproie confinée en eau douce se nourrit surtout du sang des poissons hôtes à des taux variant de 3 à 30% de son poids corporel humide·jour^{-1} (10°C). Chez cette espèce nourrie ad libitum à 10°C, l'efficacité de conversion brute estimée est de 39%. Cette efficacité relativement grande est attribuable en partie à la nature de leur régime sanguin, qui résulte en une faible perte énergétique fécale d'environ 3,4% des entrées d'énergie. Le rythme de croissance maximal se produit à 20°C chez des grandes lamproies marines de poids initial de 10–30 g et à 15°C pour les lamproies de 30–90 g. À toutes les températures d'essai (5–20°C), le taux de croissance diminue à mesure que le poids de la lamproie augmente. Des augmentations de poids de la grande lamproie marine et à des températures de l'eau allant jusqu'à 20°C entraînent une augmentation du taux de mortalité de l'hôte, ce qui laisse penser que dans des conditions naturelles, la mortalité est saisonnière. Les grandes lamproies marines confinées en eau douce montrent une préférence pour des régions spécifiques de leurs hôtes, choisissent le plus souvent des hôtes de grande taille et ne sont pas attirées par des hôtes sur lesquels d'autres lamproies se nourrissent. De telles stratégies servent à porter au maximum l'absorption de nourriture et à prolonger la survie de l'hôte, tout en assurant une nourriture à contenu énergétique uniforme.

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OF the 38 species of living lampreys representing several genera, 9 pass through a marine phase during which they feed predominantly on teleost hosts (Potter 1980). The other species are found only in fresh water. Seven of these freshwater species are parasitic and are generally confined to a single large drainage basin. In addition, three species of anadromous lampreys have given rise to landlocked forms which feed on freshwater teleosts. The remaining species are nonparasitic or brook lampreys which do not feed after metamorphosis.

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In this paper I review the nature and amount of food consumed by adult sea lampreys and provide comparisons with other species where possible.

Downstream Migration and Onset of Feeding

Applegate (1950) found that downstream movement of landlocked sea lampreys (*Petromyzon marinus*) in tributaries of Lake Huron began during the last week of October and 1st wk of November and extended through winter until early April. Both Applegate (1950) and Johnson and Anderson (1980) have demonstrated from the sizes of recently metamorphosed sea lampreys captured in lakes Superior, Michigan, and Huron, that some growth occurs during the November–May period indicating that sea lamprey feeding probably begins soon after their entry into the Great Lakes.

For anadromous sea lampreys, downstream migration in north Atlantic coastal rivers takes place during late autumn, early winter, and the following spring (Hildebrand and Schroeder 1928; Bigelow and Schroeder 1948; Davis 1967; Potter and Beamish 1977). R. J. Beamish (1980) found that the Pacific lamprey (*Lampetra tridentata*) leaves Canada's west coast rivers from late fall or early winter until June the following year and that the downstream migration of the North American river lamprey (*L. ayresii*) in these rivers occurs from May until July. Hardisty and Potter (1971) believe that the European river lamprey (*L. fluviatilis*) moves towards estuaries in western European watersheds of the Atlantic and Mediterranean between late winter and early summer.

During downstream movement, anadromous sea lampreys in the Saint John River system (New Brunswick) attack alewives (*Alosa pseudoharengus*), American shad (*Alosa sapidissima*), and white suckers (*Catostomus commersoni*) (Beamish and Potter 1975). Potter and Beamish (1977) concluded that sea lampreys in this system start feeding in brackish water or the sea during autumn or alternately in freshwater the following spring. Such variation in timing of onset of feeding agrees with the observations of Davis (1967) that anadromous *P. marinus* in Maine begins feeding between October and February or between May and June.

Body Size and Duration of the Parasitic Phase

Hardisty and Potter (1971) concluded that intraspecific variability in body size and major size differences between parasitic species may be attributable to variability in the duration of parasitic feeding. These authors divide the parasitic species into three broad groups based on the characteristic body sizes of the sexually mature adults:

i) Freshwater species such as the Hungarian lamprey (*Eudontomyzon danfordi*), the silver lamprey (*Ichthyomyzon unicuspis*), the chestnut lamprey (*I. castaneus*), and the Mexican lamprey (*Tetrapleurodon spadiceus*), which range in length from 200 to 300 mm, generally feed for less than 1 yr.

ii) Anadromous species such as the short-headed lamprey (*Mordacia mordax*), *L. fluviatilis*, and the Arctic lamprey (*L. japonica*), which vary in body length from 250 to 500 mm and whose movements may be confined to coastal regions, have a parasitic phase estimated as about 18 mo. The landlocked form of *P. marinus* is included in this category. The anadromous species *L. ayresii* attains a length of about 250 mm but feeds for less than 1 yr (R. J. Beamish 1980).

iii) The parasitic phase of the largest anadromous species such as *P. marinus*, the wide-mouthed lamprey (*Geotria australis*), and *L. tridentata*, which reach lengths of 600–900 mm, was estimated to be 18 mo and possibly as long as 30 mo. A more recent estimate of the length of the feeding phase of *P. marinus* is 23–28 mo (F. W. H. Beamish 1980). R. J. Beamish (1980) estimates that some individuals of *L. tridentata* may spend up to 42 mo in salt water before returning to freshwater.

Host Species

In the three upper Great Lakes, invasion by the sea lamprey was followed by an acute decline in some fish populations. Lake trout (*Salvelinus namaycush*) were almost eliminated in lakes Huron and Michigan because the initial predation was on the large, coldwater species (Smith 1971). Populations of burbot (*Lota lota*), rainbow trout (*Salmo gairdneri*), and lake whitefish (*Coregonus clupeaformis*) also declined. Information on the effects of sea lampreys on other species is fragmentary but wounds have been found on all except a few of the smallest species in the Great Lakes (Smith 1971).

The indirect effects of the lamprey invasion on the species succession of smaller fishes have been documented by Smith (1968). In Lake Michigan, native species in the commercial catch were lake trout, lake herring (*Coregonus artedii*), lake whitefish, and seven species of ciscoes (*Coregonus* spp.). The depletion of lake trout and burbot by sea lampreys favored their prey, the ciscoes, whose production increased. The ciscoes then received the impact of the lamprey predation because they were the predominant host in deep water. The reductions in the cisco populations favored an increase in the alewife. Its domination of the fish stocks and its occupation of various areas and depths at different periods of the year have had an adverse effect on several other species, including yellow perch (*Perca flavescens*), emerald shiner (*Notropis atherinoides*), and rainbow smelt (*Osmerus mordax*) (Smith 1968).

When host preferences of the landlocked sea lamprey were examined in a large tank, the pattern of preference did not always correspond to that seen in the Great Lakes, suggesting that the thermal distribution of host species in the lakes and their relative size are of particular importance in determining lamprey predation (Farmer and Beamish 1973).

Of the 74 species of fish found in the Lake Cayuga basin, none were immune from predation by *P. marinus* except those too small to provide sufficient area for attachment and support (Surface 1898). Hosts of importance were the brown bullhead (*Ictalurus nebulosus*), suckers (*Catostomus* spp.), carp (*Cyprinus carpio*), lake herring, and chain pickerel (*Esox niger*). Also mentioned were lake sturgeon (*Acipenser fulvescens*), lake whitefish, northern pike (*Esox lucius*), lake trout, and yellow walleye (*Stizostedion vitreum vitreum*). Even the heavy-scaled, longnose gar (*Lepisosteus osseus*) was sometimes attacked.

Adult *I. castaneus* attack a number of species of stream fishes (Hall 1960) including brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), rainbow trout, northern pike, chain pickerel, carp, white suckers, channel catfish (*Ictalurus punctatus*), and largemouth bass (*Micropterus salmoides*). Similarly, silver lampreys (*I. unicuspis*) will attack several different hosts. Scars from this species were observed on 11 species of fishes in Quebec (Vladykov and Roy 1948).

Information on the feeding habits of anadromous lampreys is rather limited but there are indications that they are not, to any great extent, specific in their choice of hosts (Hardisty and Potter 1971). The anadromous sea lamprey is reported to attack Atlantic cod (*Gadus morhua*), Atlantic herring (*Clupea harengus harengus*), haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius virens*), red hake (*Urophycis chuss*), sturgeons (*Acipenser* spp.), Atlantic mackerel (*Scomber scombrus*), Atlantic salmon (*Salmo salar*), swordfish (*Xiphias gladius*), and even basking sharks (*Cetorhinus maximus*) (Bigelow and Schroeder 1948; Scott and Crossman 1973). F. W. H. Beamish (1980) reports that sea lampreys may also attack striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*), and weakfish (*Cynoscion regalis*). Hosts of *L. tridentata* include sockeye salmon (*Oncorhynchus nerka*), pink salmon (*O. gorbuscha*), rainbow trout, and coho salmon (*O. kisutch*) (Scott and Crossman 1973), while Novikov (1963) reports that a number of teleost species other than salmonids are hosts in the Bering Sea. Similarly, *L. japonica*, *L. fluviatilis*, and *M. mordax* are reported to attack several species of teleosts (Hardisty and Potter 1971). *Lampetra ayresii* feeds on Pacific herring (*Clupea harengus pallasi*), northern anchovies (*Engraulis mordax*), and the young of five species of Pacific salmon (R. J. Beamish 1980; Roos et al. 1973).

Feeding Mechanisms

Food of the landlocked sea lamprey generally consists of blood, other body fluids, and products of tissue cytolysis (Gage 1928; Lennon 1954; Farmer et al. 1975). The structure and functions of the feeding and respiratory apparatus in lampreys and the mechanism by which they attach to hosts by the oral disc have been described by a number of authors (Dawson 1905; Reynolds 1931; Lennon 1954; Hardisty and Potter 1971; Randall 1972). Ventilation of the gills is tidal; water enters and leaves each gill pouch via a single opening, the external branchiopore allowing the adult to attach by its oral disc to either a host or the substrate. The basic suction mechanism is a change in the volume of the space enclosed by the buccal funnel (Hardisty and Potter 1971). The initial wound is made by the tonguelike piston which has two sets of plates at the oral end bearing denticles which form cutting edges. A rasping effect produced by the tongue is largely responsible for the initial destruction of host tissue (Dawson 1905). The buccal glands first develop at metamorphosis as invaginations of the oral epithelium; a process which eventually leads to the formation of paired sacs. A duct runs forward from each sac to open into the oral cavity. The secretion termed lamphredin is probably forced into these ducts by contraction of the prominent constrictor muscles of the glands (Lennon 1954) and plays an important role in feeding because of its anticoagulant properties and cytolytic effects on the skeletal muscle, blood vessels, connective tissue, and integument of hosts (Lennon 1954; Baxter 1956). The mechanism by which food material is forced towards the esophagus has been described by Dawson (1905) and Reynolds (1931).

The short narrow esophagus lies above the respiratory canal and is followed by a straight intestine with a typhlosole. The absence of a stomach is presumed to be a primitive feature. Barrington (1942) has correlated the appearance of this organ in gnathostomes with the development of macrophagy. Lampreys possess a liver whose organization is similar in principle to that of gnathostomes, although in adult lampreys the gall bladder is lost and fat stores are laid down in the hepatic tissue (Barrington 1972). None of the surviving cyclostomes (lampreys and hagfishes) possess a pancreas that is morphologically isolated from the intestine. Barrington (1972) has concluded that carbohydrate metabolism in lampreys is regulated by insulin produced by the pancreas. In mammals, alimentary activity is regulated by a combination of neural and hormonal factors. Barrington (1972) has presented evidence indicating that some form of hormonal regulation of alimentary activity is present in the intestine of lampreys.

Observations of landlocked sea lampreys in the laboratory suggest that this species relies, to some extent, on vision to locate potential hosts (Lennon 1954; Parker and Lennon 1956; Farmer and Beamish 1973). The latter authors demonstrated that when sea lampreys were given a choice of hosts of different weight but of the same species, they selected the largest individuals most frequently. Sea lampreys also showed a specificity of site of attachment; a phenomenon corroborated by field studies (Wigley 1959; Berst and Wainio 1967; Potter and Beamish 1977). The neurophysiology of orientation in lampreys is unknown except for some responses produced by the vestibular system (Rovainen 1980). Although the well-developed eyes of adult lampreys suggest that patterned vision is present in these animals, the responses of individual neurons in the retina or optic tectum have not been tested (Rovainen 1980).

Orientation by olfaction is by trial and error sampling and is therefore slow (Rovainen 1980). However, the well-developed olfactory system of *P. marinus* indicates that olfaction plays an important role in the life of this species (Kleerekoper 1972). The addition to the water supply of a sample of water in which a teleost had been held resulted in greatly increased locomotor activity by landlocked sea lampreys (Kleerekoper and Mogensen 1963; Kleerekoper 1967). When the "host water" was introduced into a single compartment of a tank, the number of entries by lampreys into that compartment increased, indicating a preference for the host odor. The response showed seasonal variation and was strongest during summer and autumn (June to December) but disappeared at the approach of sexual maturity. A number of chemical components of host water were isolated and, of the several amines present, isoleucine methyl ester proved effective in eliciting locomotor responses in landlocked *P. marinus* (Kleerekoper and Mogensen 1963; Kleerekoper 1972). In another laboratory experiment, F. W. H. Beamish (University of Guelph, Guelph, Ont., personal communication) found that ethylene diamine was effective in attracting landlocked sea lampreys.

Feeding Behavior and the Physiology of Feeding

FOOD MATERIAL AND RATE OF INTAKE

In addition to blood, other body fluids and the products of tissue cytolysis, eggs (Bigelow and Schroeder 1953), and a 150-mm fish (Penczak 1964, cited in Hardisty and Potter 1971) have also been reported in the gut contents of the anadromous sea lamprey. Among the gut contents of *L. fluviatilis* have been found various fish tissues and organs in addition to blood (Bigelow and Schroeder 1948; Eglite 1958; Zanandrea 1959). Although the presence of a whole fish in the gut contents is difficult to explain, eggs and pieces of various organs can be ingested after penetration of the host's body cavity. Grossu et al. (1962) suggested that *E. danfordi* may equally feed on live fish or carrion and R. J. Beamish (1980) observed that *L. ayresii* feeds by removing pieces of tissue and portions of fins, gut, and internal organs, demonstrating that species differences exist in the mode of feeding.

Because of the destructive effects of the landlocked sea lamprey on fish stocks in the upper Great Lakes, most research into the physiology of lamprey feeding has been devoted to this species. Gage (1928), Lennon (1954), and Farmer et al. (1975) concluded that the principal food of adult sea lampreys is blood and the latter authors estimated that the products of tissue cytolysis comprised less than 2% of the total amount of food ingested by the lampreys used in their experiments. In that study, landlocked sea lampreys held at 10°C were allowed to feed on rainbow trout and lake trout whose red blood cells had been labeled with radioactive chromium (^{51}Cr). The loss of radioactivity by trout provided an estimate of the quantity of blood consumed by lampreys. The estimates for lampreys of 16–155 g ranged from 3 to 30% of their wet body weight$\cdot d^{-1}$ with a geometric mean value of 11.6% $\cdot d^{-1}$ ($n = 31$).

Although daily intakes of 20–30% body weight observed for one-quarter of the lampreys appear high compared with maximum intakes by other fishes (for example, the crucian carp (*Carassius carassius*) feeding on roe consumed 21% body weight$\cdot d^{-1}$; the roach (*Leuciscus rutilus*) on a diet of chironomid larvae consumed 15% body weight in a 2-h period [Ivlev 1961]; and 8-g largemouth bass fed emerald shiners consumed 14% $\cdot d^{-1}$, while 150-g bass consumed 6% [Niimi and Beamish 1974]), this may be related to the nature of their food material and its rate of digestion. Thus, the percentage moisture of the blood of trout acting as hosts for lampreys increased from the norm of 85 to 96% prior to their death, while the energy content of their blood decreased from 3.2938 to 0.5342 kJ$\cdot$g wet weight^{-1} (Farmer et al. 1975). Because animals eat to satisfy their energy demand (Mayer 1955; Rozin and Mayer 1961), the high moisture content and decrease in energy content of host blood may necessitate the relatively high daily intakes of 20–30% $\cdot d^{-1}$ observed for some lampreys (Farmer et al. 1975).

To enable comparison with other species, lamprey food intake was also examined on a dry weight basis (dry food weight/dry lamprey weight × 100). Intakes expressed in this manner ranged from 2.0 to 16.3% $\cdot d^{-1}$, with a geometric mean of 6.9% $\cdot d^{-1}$ and did not appear to be influenced by lamprey weight (Table 1). In comparison, the maximum daily intake of sockeye salmon at 15°C decreased as a log–log function of dry body weight falling from an average of 16.9% for a 4-g fish to 4.3% for a 216-g fish (Brett 1971). Davis and Warren (1971) found young chinook salmon (*O. tshawytscha*) could consume up to 20% $\cdot d^{-1}$ on a dry weight basis and Farmer et al. (1979) found that when 15-g Atlantic salmon were fed to satiation once daily at 10°C, they consumed 5–6% $\cdot d^{-1}$. The food intake of lampreys expressed in this manner is generally comparable to values observed for other fishes but did not show a decrease with increasing lamprey weight. This may have been attributable to an increase in the host-to-lamprey weight ratio among the larger lampreys (Table 1). Possibly, the size of a lamprey relative to its host influences lamprey feeding efficiency.

In a laboratory study, Farmer et al. (1977) showed that the rate of host mortality (white suckers) in-

TABLE 1. Daily blood consumption at 10 ± 1°C by landlocked sea lampreys feeding on rainbow and lake trout.[a]

Lamprey weight class, g	Mean lamprey weight, g	No. of animals	Mean blood consumption and ranges, % body weight·d^{-1}[b]		Ratio of host weight[b] to lamprey weight
			Wet	Dry	
16–50	31.2	17	11.2 (4.3–29.0)	6.7 (2.9–16.3)	9.8
51–85	68.1	6	10.2 (2.9–21.0)	6.3 (2.0–16.0)	8.3
86–120	96.6	3	15.1 (9.4–29.8)	8.3 (6.2–14.7)	12.3
121–155	138.4	5	14.7 (8.1–23.3)	7.8 (5.3–12.1)	17.0

[a] From Farmer et al. (1975).
[b] Geometric means.

creased with lamprey weight and water temperature (Fig. 1). At temperatures of 5 and 10°C, host mortality increased with lamprey weight over the 10- to 90-g range, whereas at 15 and 20°C mortality increased with weight reaching a maximum for animals of 50–70 g before declining. Decreases in host mortality at the highest temperature may reflect a suppression of appetite among the larger lampreys (Farmer et al. 1977). For smaller lampreys (10–50 g), temperature increases of 5°C within the 5–20°C range resulted in a doubling of the rate of host mortality. While rising temperature also resulted in greater host mortality by the larger lampreys (50–90 g), the magnitude of the change was not as pronounced as from the feeding activities of the smaller animals. Changes in the rate of host mortality over the 10–20°C range (Fig. 1) indicate that the mean food intake of 11.6% wet weight·d^{-1} observed by Farmer et al. (1975) for lampreys at 10°C would be exceeded at the higher temperatures.

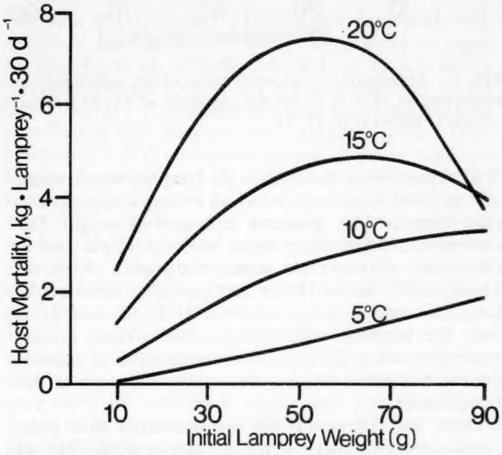

FIG. 1. Rates of host mortality (white suckers) at temperatures of 5–20°C resulting from the feeding activities of sea lampreys of 10–90 g initial weight (Farmer et al. 1977).

The marked effect of water temperature and lamprey weight on rate of host mortality suggests that mortality under natural conditions is seasonal. Applegate (1950) observed that sea lampreys feeding in the deeper waters of Lake Huron (60–150 m) during the April–June period only increased from 16 to 22 g before moving to shallower, warmer waters (≤40 m) during the summer where they increased to 153 g by October. Temperatures at 60–150 m during April–June ranged from 3 to 5°C and those within the thermocline at depths of ≤40 m during the summer and early fall generally from 6 to 16°C (Ayers et al. 1956; McCombie 1967; Spangler and Berst 1976). The increased growth rate during the June–October period must reflect increased lamprey feeding activity. Accordingly, Spangler (1970) observed that the greatest reduction of lake whitefish in Lake Huron occurred between June and November and was correlated with a peak in lamprey feeding activity. Fresh lamprey marks on splake (*S. fontinalis* × *S. namaycush*) captured in Lake Huron were minimal in the spring and early summer and increased in frequency until September when more than 20% of the fish examined bore fresh marks (Berst and Spangler 1970). Similarly, Wigley (1959) found that sea lamprey feeding activity in Cayuga Lake reached a peak during August and September.

CONVERSION EFFICIENCIES

The energy and moisture content of blood from three host species was determined by Farmer et al. (1975, 1977):

	Moisture content, %[a]	kJ·g dry wt^{-1}
Salmo gairdneri	84.6 (12)	21.39 (7)
Salvelinus namaycush	85.9 (4)	21.76 (4)
Catostomus commersoni	84.6 (50)	23.04 (25)

[a] Number of determinations in parentheses.

For comparison, the mean energy values were seen to fall within the range given by Davis and Warren (1971) for different fish food organisms. Farmer et al.

(1975) determined that the mean moisture content of juvenile sea lampreys was 79.7% and their energy content 25.24 kJ·g dry weight^{-1}. Gross conversion efficiencies in energy equivalents were then estimated for lampreys of 28–157 g which consumed trout blood at rates of 3–22% wet body weight·d^{-1} during intervals of 4–14 d. Because the energy content of trout blood (rainbow and lake trout) changed in response to lamprey feeding activity, a correction was necessary when estimating lamprey energy intake. Excepting one relatively high value, efficiencies at 10°C ranged from 11 to 50% with a mean of 39% ($n = 15$). The mean fecal energy loss for seven of the lampreys was 3.4% of the energy of the blood they consumed.

Although some variability was introduced into the efficiency values because blood intake was estimated using a radioisotope method, small amounts of host tissue fluid might have contributed to lamprey energy intake, and energy of trout blood changed in response to lamprey feeding; the mean efficiency of 39% for lampreys, while high compared to values for other fishes (Brett and Groves 1979), is a reasonable estimate for this animal. In their calculations of the average partitioning of dietary energy of young carnivorous fishes feeding above maintenance level, Brett and Groves (1979) suggest that 20% of intake energy is lost as feces and that an average of 29% of this energy is available for growth. Depending on metabolic rate, from 0 to 45% of intake energy can be partitioned for growth. This suggests that lampreys are able to attain the relatively high conversion efficiency of 39% because of the nature of their diet which results in small fecal energy losses. The mean conversion efficiency for sea lampreys at 10°C has been exceeded by young, immature fishes (for example, 55% for 1- to 2-g coho salmon feeding at 8–14°C on live fly larvae [Averett cited in Brett and Groves 1979]; and 52% for the two-spotted cichlid (*Cichlasoma bimaculatum*) feeding ad libitum at 28°C on *Tubifex* [Warren and Davis 1967]) and equaled by some other fishes (for example, 43% for 100-g largemouth bass held at 25°C and fed emerald shiners [Niimi and Beamish 1974; Beamish et al. 1975]; 38% for 56-g tarpon (*Megalops cyprinoides*) at 28°C and feeding on mosquitofish (*Gambusia affinis*) [Pandian 1967]; and 39% for yearling reticulate sculpin (*Cottus perplexus*) fed optimal rations of midge larvae and held at temperatures of 8–15°C [Warren and Davis 1967]).

THE INFLUENCE OF WATER TEMPERATURE ON GROWTH RATE

The influence of water temperature on the instantaneous growth rate of the landlocked sea lamprey was determined by Farmer et al. (1977) in laboratory tanks by allowing lampreys to feed ad libitum on white suckers, a common host species (Coble 1967). Maximum growth rates occurred at 20°C for 10- to 30-g lampreys and at 15°C for animals of 30–90 g (Fig. 2). Rates at 5°C were minimal throughout the lamprey weight range and at 10°C intermediate. At all temperatures, growth rates decreased as lampreys increased in weight. Decreases in food intake relative to body weight and in conversion efficiency accompany the growth of teleosts (Brett 1971; Kelso 1972) and probably account for the small decline in growth rate at 5, 10, and 15°C over the lamprey weight range. While these mechanisms also act at 20°C, a slight suppression of appetite among the larger lampreys probably occurred at this temperature.

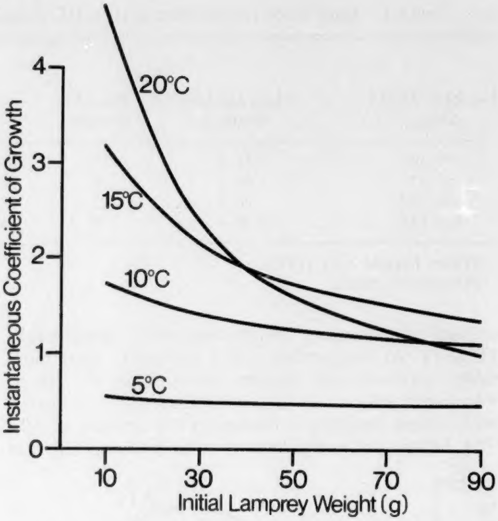

FIG. 2. Instantaneous growth rates (30-d intervals) at temperatures of 5–20°C for sea lampreys of 10–90 g initial weight (Farmer et al. 1977).

Brett and Higgs (1970) demonstrated that gross conversion efficiency, appetite, and growth rate of fingerling sockeye salmon increased with temperature to 15°C and then declined with further increases in temperature to 24°C. The slow rate of digestion at low temperatures limited appetite and thus growth, while at high temperatures the combination of declining appetite and conversion efficiency coupled with increases in metabolic expenditure were limiting for growth. Data presented in Fig. 1 and 2 suggest that temperature has a similar influence on these processes in lampreys. Accordingly, Smith (1972) has suggested that salmonids share similar thermal requirements with the landlocked sea lamprey, while Beamish (1973) showed that the standard oxygen consumption of adults of this species was not appreciably different from rates recorded at corresponding temperatures for salmonids of similar size.

Instantaneous growth rates during 30-d intervals were calculated for sea lampreys in Lake Huron from

TABLE 2. Instantaneous growth rates (*G*) of sea lampreys in Lake Huron and in the laboratory at temperatures of 5, 10, and 15°C.

Growth interval (Lake Huron)	*W* increase (g) (Lake Huron)[a]	*G* (Lake Huron)[b]	*G* (Laboratory)[c] 5°C	10°C	15°C
Apr.–May	15.9–18.6	0.523	0.542	1.598	2.728
May–Jun.	18.6–22.4	0.620	0.535	1.552	2.578
Jun.–Jul.	22.4–40.1	1.940	0.526	1.497	2.407
Jul.–Aug.	40.1–80.4	2.320	0.501	1.332	1.921
		1.575[d]			
Aug.–Sept.	80.4–103.2	0.833	0.471	1.151	1.432
Sept.–Oct.	103.2–152.6	1.303	0.459	1.087	1.277
Oct.–Nov.	152.6–171.3	0.383	0.433	0.996	1.054
Nov.–Dec.	171.3–169.6	—	—	—	—

[a] Weights (*W*) from Applegate (1950).
[b] Calculated from Applegate (1950).
[c] Calculated from Farmer et al. (1977).
[d] July–Sept. growth rate.

the data of Applegate (1950) and compared with values of Farmer et al. (1977) for animals of equal weight (Table 2). Growth rates in Lake Huron during April–June were comparable to rates observed in the laboratory at 5°C in agreement with Applegate's (1950) observation that lampreys fed in deeper waters (60–150 m) of 3–5°C during this period. Between June and October, growth rates in Lake Huron increased and were similar to rates recorded in the laboratory at 10–15°C, reflecting the presence of lampreys in warmer, shallower water (≤40 m) of 6–15°C (Applegate 1950). The decline in growth rate for lampreys in Lake Huron during October–November probably reflects the cooling of the lake at that time. Accordingly, Johnson and Anderson (1980) observed that, of the sea lampreys captured in lakes Michigan and Superior, there was a continuous decrease after October in the proportion of individuals whose guts contained food material. In agreement with the observations of Applegate (1950) for lampreys in Lake Huron, these authors found that recently metamorphosed lampreys (≤200 mm in length) were captured by deepwater fisheries and that larger lampreys (>251 mm) were generally captured in shallow, inshore waters.

HOST–LAMPREY INTERACTIONS

Despite the efficiency of the circulatory system of bony fishes, their small blood volume (3% body weight, compared with 7–9% in mammals [Holmes and Donaldson 1969; Prosser et al. 1950]) makes them susceptible to the effects of lamprey attack. Lennon (1954) demonstrated that the mean red cell count in mortally wounded white suckers was reduced by 84% from the mean for uninjured fish, but that they were able to manufacture leucocytes faster than they were removed by lampreys. Similarly, Farmer et al. (1975) observed that hematocrit readings for trout dying from the feeding of lampreys were markedly reduced (mean 2.0%) compared to readings for control fish (mean 35.0%). Because of the removal of red blood cells, the mean percentage moisture of their blood increased from 84.5 to 96.4%. Despite these changes, the mean plasma osmolarity of dying trout (315 mOsmol·L^{-1}) was not much different from that of control trout (341 mOsmol·L^{-1}). Although hosts are able to retain their osmotic balance by transferring of ions from other body compartments, some are unable to manufacture red blood cells at rates equal to their removal. Presumably, the blood volume of trout remains constant during lamprey feeding because of the osmotic influx of water in the freshwater medium.

Observations of a large experimental tank showed that sea lamprey attacks resulting in death of lake trout were most common (54%) and that in some instances (9% of attacks) lampreys fed on trout then detached before killing their host. A relatively large proportion of the attacks (37%) resulted in detachment of lampreys before feeding was initiated. The attachment time of lampreys that killed their hosts was a function of the host's survival time with the longest period being 14 d. The lampreys that detached after feeding without killing their hosts were attached from 1 to 13 d. Attachment times of nonfeeding lampreys ranged from ¼ d to 18 d. The significance of nonfeeding attachments is unknown. Presumably, this behavior allows satiated lampreys to eliminate the energy expenditure associated with locomotion. In this context, Beamish (1974) suggested that the swimming performance of landlocked sea lampreys was poor compared with that of teleosts because of the absence of a hydrostatic organ, a reduced stability because of the absence of paired fins, and the lack of propulsive thrust provided by the reduced caudal fin. Lennon (1954) found that, of the total number of sea lamprey attachments to freshwater teleosts held in laboratory tanks, only 9.2%

were of the nonfeeding type. The detachment of lampreys from living hosts after feeding allows host survival and may be a response to changes in the moisture and energy content of the lamprey's diet or to satiation. Presumably, locomotory energy expenditure during search for new hosts is reduced because teleosts to not appear to avoid lamprey attack (Farmer and Beamish 1973).

Laboratory studies indicate that *P. marinus* most frequently attacks freshwater teleosts below the lateral line in the area between the head and caudal peduncle (69% of attacks) (Farmer and Beamish 1973). Of these attacks, almost half are in the area of the pectoral fins. Fewer attacks occur above the lateral line (17%) or on the head (10%). Attacks on the caudal peduncle or on the fins are rare. A similar pattern of scarring from the landlocked sea lamprey has been reported on lake trout in Lake Cayuga (Wigley 1959) and on rainbow trout in Lake Huron (Berst and Wainio 1967). Scarring of Atlantic salmon by the anadromous sea lamprey was predominantly (84%) on their ventral surface between the operculum and caudal peduncle (Potter and Beamish 1977), and R. J. Beamish (1980) observed that *L. tridentata* also attacks hosts on their ventral surface most commonly near the pectoral fins. A selection of feeding sites on the ventral area of hosts, particularly near the pectoral fins, may be related to the thinner muscular layer, the less dense scaling and the greater distribution of blood in this area (Farmer and Beamish 1973). The preferred area on hosts seems to differ for those species that consume greater proportions of muscle tissue. Thus, both *L. ayresii* and *L. fluviatilis* are reported to show a preference for the area above the lateral line (R. J. Beamish 1980; Maitland 1980).

Lennon (1954) reported that a host struggling to dislodge a lamprey frequently draws other lampreys to itself. This behavior would decrease duration of host survival, lamprey feeding time, and hence growth rate. Thus, the relative numbers of single and multiple attacks on white suckers of similar size were examined in a large tank to determine if nonfeeding sea lampreys were attracted to teleosts serving as hosts (Farmer and Beamish 1973). When a hypothetical binomial distribution describing the relation between single and multiple attacks was compared to the observed distribution, they were not significantly different (Fig. 3). Thus, it was concluded that the attachment of one or more lampreys on a given host does not attract other lampreys to that host. The general pattern of multiple attack frequency was similar to that shown by the anadromous sea lamprey feeding on Atlantic salmon (F. W. H. Beamish 1980).

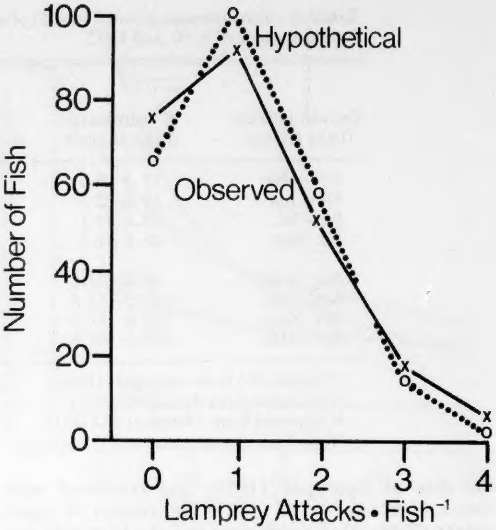

FIG. 3. Observed and hypothetical distributions of single and multiple attacks on white suckers of similar size (Farmer and Beamish 1973).

The higher incidence of attack on larger hosts under laboratory conditions (Farmer and Beamish 1973) parallels field results in which scarring rate by *P. marinus* has been correlated with size of fish for splake (Berst and Spangler 1970), white sucker (Hall and Elliott 1954; Coble 1967), rainbow trout (Berst and Wainio 1967), lake trout (Wigley 1959), kokanee salmon (Collins 1971), and Atlantic salmon (Potter and Beamish 1977). Although these field observations could simply have reflected greater mortality among smaller hosts, the data of Budd et al. (1969) indicate that, under natural conditions, landlocked sea lampreys select larger hosts. Thus, before age IV, annual mortality of lake trout planted in Lake Huron did not differ from annual mortalities observed for lake trout populations in the absence of sea lampreys (Budd et al. 1969). Thereafter, the annual mortality rate rose sharply and the population disappeared at age VI or VII. There was little evidence of lamprey attacks on lake trout less than 43–46 cm.

Duration of host survival is dependent on blood loss in relation to blood volume. Farmer et al. (1975) observed that trout (rainbow and lake trout) losing daily amounts of blood equivalent to their blood volume died in less than 2 d and those losing the equivalent of 25% daily died in 14 d (Fig. 4). Estimated times to death for trout losing daily amounts equivalent to 10% blood volume were of such duration to suggest that these hosts were able to replenish lost blood constituents and survive. Thus, for a given rate of lamprey blood intake, the duration of host survival must increase with increases in the host-to-lamprey weight ratio. Using the mean feeding rate of 12% wet body weight$\cdot$d^{-1} observed for lampreys at 10°C, a trout blood volume of 3% body weight and the relationship between host blood loss and time to death (Fig. 4), Farmer et al. (1975) estimated that a host-to-lamprey weight ratio

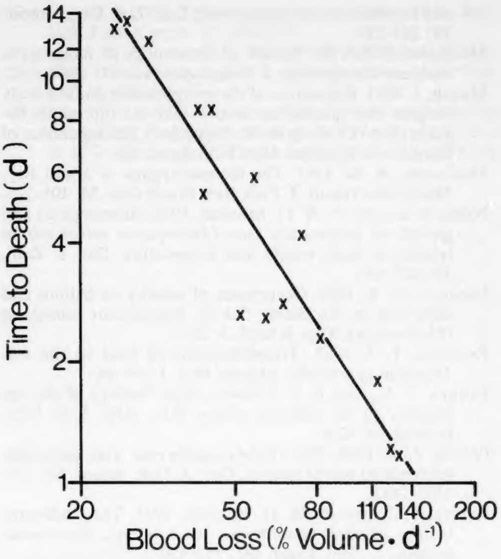

FIG. 4. The relationship between time to death for trout and daily blood loss expressed as a percentage of blood volume (Farmer et al. 1975).

of at least 40:1 was necessary for host survival. However, they indicated that lamprey feeding rates at temperatures other than 10°C would vary and thus alter this ratio as would lamprey detachments from living hosts.

In summary, the pattern of multiple attack frequency by *P. marinus* on teleosts and their selection of specific areas on larger hosts serves to maximize food intake and duration of feeding while ensuring food material of a more constant energy content. Host survival is augmented, to some extent, by lamprey detachments from living hosts. Subsequent locomotory energy expenditure by lampreys during search for new hosts may be reduced as teleosts do not appear to avoid lamprey attack.

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Applegate, V. C. 1950. Natural history of the sea lamprey, *Petromyzon marinus*, in Michigan. Spec. Rep. U.S. Fish Wildl. Serv. 55: 237 p.

Ayers, J. C., D. V. Anderson, D. C. Chandler, and G. H. Lauff. 1956. Currents and water masses of Lake Huron. Ont. Dep. Lands Forests. Div. Res. Rep. 35.

Barrington, E. J. W. 1942. Gastric digestion in the lower vertebrates. Biol. Rev. 17: 1–27.

1972. The pancreas and intestine, p. 135–170. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. II. Academic Press, London and New York.

Baxter, E. W. 1956. Observations on the buccal glands of lampreys (*Petromyzontidae*). Proc. Zool. Soc. Lond. 127: 95–118.

Beamish, F. W. H. 1973. Oxygen consumption of adult *Petromyzon marinus* in relation to body weight and temperature. J. Fish. Res. Board Can. 30: 1367–1370.

1974. Swimming performance of adult sea lamprey, *Petromyzon marinus*, in relation to weight and temperature. Trans. Am. Fish. Soc. 2: 355–358.

1980. Biology of the North American anadromous sea lamprey, *Petromyzon marinus*. Can. J. Fish. Aquat. Sci. 37: 1924–1943.

Beamish, F. W. H., A. J. Niimi, and P. F. K. P. Lett. 1975. Bioenergetics of teleost fishes: environmental influences, p. 187–209. *In* L. Bolis, H. P. Maddrell, and K. Schmidt-Nielsen [ed.] Comparative physiology — functional aspects of structural materials. North-Holland Publishing Co., Amsterdam.

Beamish, F. W. H., and I. C. Potter. 1975. The biology of the anadromous sea lamprey (*Petromyzon marinus*) in New Brunswick. J. Zool. Lond. 177: 57–72.

Beamish, R. J. 1980. Adult biology of the river lamprey (*Lampetra ayresi*) and the Pacific lamprey (*Lampetra tridentata*) from the Pacific coast of Canada. Can. J. Fish. Aquat. Sci. 37: 1906–1923.

Berst, A. H., and G. R. Spangler. 1970. Population dynamics of F_1 splake (*Salvelinus fontinalis* × *S. namaycush*) in Lake Huron. J. Fish. Res. Board Can. 27: 1017–1032.

Berst, A. H., and A. A. Wainio. 1967. Lamprey parasitism of rainbow trout n southern Georgian Bay. J. Fish. Res. Board Can. 26: 2413–2424.

Bigelow, H. B., and W. C. Schroeder. 1948. Fishes of the western North Atlantic. 2. Cyclostomes. Mem. Sears Fdn, Mar. Res. 1: 29–58.

1953. Fishes of the Gulf of Maine. Fishery Bull. Fish. Wildl. Serv. U.S. 53: 577 p.

Brett, J. R. 1971. Satiation time, appetite and maximum food intake of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 28: 409–415.

Brett, J. R., and T. D. D. Groves. 1979. Physiological energetics, p. 279–352. *In* W. S. Hoar, D. J. Randall, and J. R. Brett [ed.] Fish physiology. Vol. 8. Academic Press Inc. New York, San Francisco, and London.

Brett, J. R., and D. A. Higgs. 1970. Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon. *Oncorhynchus nerka*. J. Fish. Res. Board Can. 27: 1767–1779.

Budd, J. C., F. E. J. Fry, and P. S. M. Pearlstone. 1969. Final observations on the survival of planted lake trout in South Bay, Lake Huron. J. Fish. Res. Board Can. 26: 2413–2424.

Coble, D. W. 1967. White sucker population of South Bay, Lake Huron and effects of the sea lamprey on it. J. Fish. Res. Board Can. 24: 2117–2136.

Collins, J. J. 1971. Introduction of kokanee salmon (*Oncorhynchus nerka*) in Lake Huron. J. Fish. Res. Board Can. 28: 1857–1871.

Davis, G. E., and C. E. Warren. 1971. Estimation of food consumption rates, p. 227–248. *In* W. D. Ricker [ed.] Methods of assessment of fish production in fresh waters. Blackwell Scientific Publications, Oxford and Edinburgh.

Davis, R. M. 1967. Parasitism by newly transformed anadromous sea lampreys on landlocked salmon and other fishes in a coastal Maine lake. Trans. Am. Fish. Soc. 96: 11–16.

Dawson, R. M. 1905. The breathing and feeding mechanism of the lampreys. Biol. Bull. (Woods Hole, Mass.) 9: 1–21, 91–111.

Eglite, R. 1958. The feeding habits of the river lamprey, *L. fluviatilis* (L.) in the sea. Zool. Zh. 37: 1509–1514.

Farmer, G. J., D. Ashfield, and H. S. Samant. 1979. Effects of zinc on juvenile Atlantic salmon (*Salmo salar*): acute toxicity, food intake, growth and bioaccumulation. Environ. Pollut. 19: 103–117.

Farmer, G. J., and F. W. H. Beamish. 1973. Sea lamprey (*Petromyzon marinus*) predation on freshwater teleosts. J. Fish. Res. Board Can. 30: 601–605.

Farmer, G. J., F. W. H. Beamish, and P. F. Lett. 1977. The influence of water temperature on the growth rate of the landlocked sea lamprey (*Petromyzon marinus*) and the associated rate of host mortality. J. Fish. Res. Board Can. 34: 1373–1378.

Farmer, G. J., F. W. H. Beamish, and G. A. Robinson. 1975. Food consumption of the adult landlocked sea lamprey, *Petromyzon marinus* L. Comp. Biochem. Physiol. 50A: 753–757.

Gage, S. H. 1928. The lampreys of New York State — life history and economics. Rep. NY Cons. Dep. 8: 158–191.

Grossu, A., V. Homei, P. Barbu, and A. Popescu. 1962. Contribution à l'étude des *Pétromyzonides* de la République Populaire Roumaine. Trav. Mus. Hist. Nat. Gr. Antipa 3: 253–279.

Hall, A. E., and O. R. Elliot. 1954. Relationship of length of fish to incidence of sea lamprey scars on white suckers, *Catostomus commersoni*, in Lake Huron. Copeia 1: 73–74.

Hall, J. D. 1960. Preliminary studies on the biology of native Michigan lampreys. M.Sc. thesis, Univ. Michigan, Ann Arbour, MI. 39 p.

Hardisty, M. W., and I. C. Potter. 1971. The general biology of adult lampreys, p. 127–206. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London and New York.

Hildebrand, S. G., and W. C. Schroeder. 1928. Fishes of Chesapeake Bay. Bull. Bur. Fish. Wash. 43: 366 p.

Holmes, W. N., and E. M. Donaldson. 1969. The body compartments and the distribution of electrolytes, p. 1–89. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. 1. Academic Press Inc., New York and London.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, CT. 302 p.

Johnson, B. G. H., and W. C. Anderson. 1980. Predatory-phase sea lampreys (*Petromyzon marinus*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37: 2007–2020.

Kelso, J. R. M. 1972. Conversion, maintenance and assimilation for walleye, *Stizostedion vitreum vitreum*, as affected by size, diet and temperature. J. Fish. Res. Board Can. 29: 1181–1192.

Kleerekoper, H. 1967. Some aspects of olfaction in fishes with special reference to orientation. Am. Zool. 7: 385–395.

1972. The sense organs, p. 373–404. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. II. Academic Press, London and New York.

Kleerekoper, H., and J. Mogensen. 1963. Role of olfaction in the orientation of *Petromyzon marinus*. 1. Response to a single amine in prey's body odor. Physiol. Zool. 36: 347–360.

Lennon, R. E. 1954. Feeding mechanism of the sea lamprey and its effect on host fishes. Fish. Bull. U.S. Dep. Interior 98: 247–293.

Maitland, P. S. 1980. Review of the ecology of lampreys in northern Europe. Can. J. Fish. Aquat. Sci. 37: 1944–1952.

Mayer, J. 1955. Regulation of the energy intake and the body weight: the glucostatic theory and the lipostatic hypothesis, p. 15–43. *In* R. W. Miner [ed.] The regulation of hunger and appetite. Ann. N.Y. Acad. Sci.

McCombie, A. M. 1967. The thermal regime of South Bay, Manitoulin Island. J. Fish. Res. Board Can. 24: 101–125.

Niimi, A. J., and F. W. H. Beamish. 1974. Bioenergetics and growth of largemouth bass (*Micropterus salmoides*) in relation to body weight and temperature. Can. J. Zool. 52: 447–456.

Novikov, N. P. 1963. Occurrence of attacks on halibut and other fish in the Bering Sea by *Entosphenus tridentatus* (Richardson). Vop. Ikhtiol. 3: 28.

Pandian, T. J. 1967. Transformation of food in the fish *Megalops cyprinoides*. Marine Biol. 1: 60–64.

Parker, P. S., and R. E. Lennon. 1956. Biology of the sea lamprey in its parasitic phase. Res. Rep. U.S. Dep. Interior 44: 32 p.

Potter, I. C. 1980. The Petromyzoniformes with particular reference to paired species. Can. J. Fish. Aquat. Sci. 37: 1595–1615.

Potter, I. C., and F. W. H. Beamish. 1977. The freshwater biology of adult anadromous sea lampreys, *Petromyzon marinus*. J. Zool. Lond. 181: 113–130.

Prosser, C. L., D. W. Bishop, F. A. Brown, T. L. Jahn, and V. J. Wulff. 1950. Comparative animal physiology. W. B. Saunders Co., Philadelphia, PA. 888 p.

Randall, D. J. 1972. Respiration, p. 287–306. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2. Academic Press, London, New York.

Reynolds, T. E. 1931. Hydrostatics of the suctorial mouth of the lamprey. Univ. Calif. Publ. Zool. 37: 15–35.

Roos, J. F., P. Gilhousen, S. R. Killick, and E. R. Zyblut. 1973. Parasitism on juvenile Pacific salmon (*Oncorhynchus*) and Pacific herring (*Clupea harengus pallasi*) in the Strait of Georgia by the river lamprey (*Lampetra ayresii*). J. Fish. Res. Board Can. 30: 565–568.

Rovainen, C. M. 1980. Neurophysiology of lampreys. Can. J. Fish. Aquat. Sci. 37: 1723–1738.

Rozin, P., and J. Mayer. 1961. Regulation of food intake in the goldfish. Am. J. Physiol. 201: 968–974.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

Smith, B. R. 1971. Sea lampreys in the Great Lakes of North America, p. 207–248. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London, New York.

Smith, S. H. 1968. Species succession and fishery exploitation in the Great Lakes. J. Fish. Res. Board Can. 25: 667–693.

1972. Factors of ecologic succession in oligotrophic fish communities of the Laurentian Great Lakes. J. Fish. Res. Board Can. 29: 717–730.

Spangler, G. R. 1970. Factors of mortality in an exploited population of whitefish, *Coregonus clupeaformis* in northern Lake Huron, p. 515–529. *In* C. C. Lindsey and C. S. Woods [ed.] Biology of coregonid fishes. University of Manitoba Press, Winnipeg, Man.

Spangler, G. R., and A. H. Berst. 1976. Performance of lake trout (*Salvelinus namaycush*) backcrosses, F_1 splake (*Salvelinus fontinalis* × *S. namaycush*), and lake trout in Lake Huron. J. Fish. Res. Board Can. 33: 2402–2407.

SURFACE, H. A. 1898. The lampreys of central New York. Bull. U.S. Fish. Comm. 17: 209–215.

VLADYKOV, V. D., AND J. M. ROY. 1948. Biologie de la lamproie d'eau douce après la métamorphose. Rev. Can. Biol. 7: 483–485.

WARREN, C. E., AND G. E. DAVIS. 1967. Laboratory studies on the feeding, bioenergetics and growth of fish, p. 175–214. *In* S. D. Gerking [ed.] The biological basis of fresh water fish production. Blackwell Scientific Publications, Oxford and Edinburgh.

WIGLEY, R. L. 1959. Life history of the sea lamprey of Cayuga Lake, New York. Fish. Bull. U.S. Fish. Wildl. Serv. 59: 559–617.

ZANANDREA, G. 1959. *Lampetra fluviatilis* catturata in mare nel Golfo di Gaeta. Pubbl. Staz. Zool. Napoli 31: 265–307.

Physiology of Adult Lampreys, with Special Regard to Natural Starvation, Reproduction, and Death after Spawning[1]

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LARSEN, L. O. 1980. Physiology of adult lampreys, with special regard to natural starvation, reproduction, and death after spawning. Can. J. Fish. Aquat. Sci. 37: 1762–1779.

In this review I have attempted to define (1) how the genetic program responsible for migration, sexual maturation, and death after spawning is implemented via the endocrine system, and (2) to what extent environmental factors influence the implementation of the genetic program. The time of upstream migration and the body size at migration may vary enormously (e.g. in *Lampetra fluviatilis*). Whether the differences reflect different genetic backgrounds in different populations or different environmental conditions in previous stages is unknown. Migration is correlated with lack of food intake, loss of marine osmoregulatory capacity, and atrophy of the intestine. The possible endocrine control of this phase is not clear. Development of secondary sex characters, final maturation of the gonads, spermiation, and ovulation seem to depend on a gonadotropic factor secreted by the pro- and meso-adenohypophysis, but gonadotropin is not as important as in higher vertebrates. Increases in day length or in temperature do not appear to be important clues for initiating sexual maturation; rather this may depend on a metabolic signal related to starvation. The period of natural starvation, from upstream migration until death after spawning, involves atrophy or degeneration in most organs and tissues at the same time as the gonads are developing. With the exception of the intestine and the size of the liver in males, degeneration is generally slow during upstream migration. Upon sexual maturation, the changes are rapid. Energy expenditure and gonadal growth are based on mobilization of lipid and protein, mainly from the body wall. The mobilization of lipid and of protein runs in parallel, both being slow before and rapid during sexual maturation. The possible role of gonadotropin, sex hormones, and insulin in the metabolism of the starving lamprey is discussed. Other hormones seem of little importance. Little is known about the role of the autonomic nervous system in the catabolic processes. Death after spawning can be delayed considerably by hypophysectomy and seems to depend on gonadotropin in females and on some pituitary factor different from gonadotropin in males. Treatment with estradiol surprisingly prolongs life. In all cases of prolonged life induced experimentally, the rate of reduction in body length is slow, probably reflecting a reduced intensity of starvation.

Key words: physiology, starvation, reproduction, death, metabolism, migration

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Le compte rendu qui suit tente de définir (1) la manière dont le programme génétique responsable de la migration, de la maturation sexuelle et de la mort après la fraie est exécuté par le biais du système endocrinien, et (2) jusqu'à quel point les facteurs de l'environnement influent sur l'exécution de ce programme. Il peut y avoir de grandes variations de l'époque de migration vers l'amont et de la taille au moment de cette migration (e.g. chez *Lampetra fluviatilis*). On ignore si ces différences reflètent des variations dans la constitution génétique des diverses populations ou dans les conditions ambiantes à des stades antérieurs. Il y a relation entre migration et jeûne, perte de capacité osmorégulatrice en mer et atrophie de l'intestin. Le contrôle endocrinien de cette phase n'est pas clair. Le développement des caractères sexuels secondaires, la maturation finale des gonades ainsi que la sécrétion de la laitance et l'ovulation semblent dépendre d'un facteur gonadotrope sécrété par la pro- et la méso-adénohypophyse, mais ici la gonadotrophine n'est pas aussi importante que chez les vertébrés supérieurs. Des jours plus longs et des températures plus élevées ne semblent pas jouer un rôle important dans le déclenchement de la maturation sexuelle; ce phénomène dépendrait plutôt d'un signal métabolique lié au jeûne. La période de jeûne naturel, depuis la migration vers l'amont jusqu'à

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la mort après la fraie, comporte l'atrophie ou la dégénération de la plupart des organes et des tissus en même temps que se développent les gonades. Cette dégénération est généralement lente lors de la migration vers l'amont, à l'exception de l'intestin et du foie chez les mâles. Au moment de la maturation sexuelle, les changements sont rapides. La dépense d'énergie et la croissance des gonades sont fondées sur la mobilisation des lipides et des protéines, provenant en grande partie de la paroi du corps. La mobilisation des lipides et des protéines se fait en parallèle, l'une et l'autre étant lente avant et rapide pendant la maturation sexuelle. Nous examinons le rôle possible de la gonadotrophine, des hormones sexuelles et de l'insuline dans le métabolisme de lamproies pendant le jeûne. Les autres hormones semblent peu importantes. On connaît très peu le rôle du système nerveux autonome dans les processus cataboliques. L'hypophysectomie peut retarder considérablement la mort après la fraie. La mortalité semble dépendre de la gonadotrophine chez les femelles et de quelque facteur hypophysaire différent de la gonadotrophine chez les mâles. Chose surprenante, le traitement à l'oestradiol prolonge la vie. Dans tous les cas de prolongation expérimentale de la vie, le taux de rétrécissement de la longueur du corps est lent, reflétant probablement un jeûne moins sévère.

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LAMPREYS spawn in spring or summer. Development of secondary sex characters and the final growth and differentiation of egg follicles and development of spermatozoa take place a couple of weeks or months before spawning. They spawn in streams or brooks, close to areas where the larvae spend their hidden life.

It is characteristic of lampreys that they do not feed during the period of sexual maturation. Gonadal growth during this period, especially the ovaries, depends on the energy reserves. The parasitic species accumulate these reserves during the juvenile feeding stage, whereas the nonparasitic species utilize reserves accumulated by suspension feeding before metamorphosis. This phase of natural starvation or synchony ("Synchonie" was used by Mislin (1941) for the comparable phase in salmon; the word means "Liquidation" and refers to mobilization of muscle substance for use in ovarian growth — see Miescher 1880, 1890, 1892) is characterized by a dramatic remodeling of the body, drawing on fat and protein reserves, mainly in muscles and skin. This phase ends in death after spawning; in most cases death occurs within a few days or weeks after spawning.

A few other vertebrate species (e.g. eels and Pacific salmon) show such a dramatic mass death after spawning; for Pacific salmon the term "programmed death" was introduced (see Krohn 1966) to stress that death seems to be a regulated process. Of course the whole life cycle is based on a genetic program, and one of the tasks of physiologists is to try, by analysis of the time sequence and mechanisms of development, to reveal how the genetic program is implemented. The genes exert their action via the two main effector systems, the nervous and the hormonal systems, and probably also by less well-described regulatory mechanisms of a local nature, which play important roles in differentiation and maturation. Molecular biologists have spent much time elucidating how hormones act on genes, but we know nothing about how the genetic information influences hormone secretion — for instance how the secretion of hormones necessary for metamorphosis or sexual maturation is initiated. An experimental study in this interesting field has begun in the southern platyfish (*Xiphophorus maculatus*) in which genetic analysis is helped by the fact that genes for early and late sexual maturation are linked to pigment genes that serve as genetic markers (Schreibman and Kallman 1978). Another important task of physiologists is to define how and to what extent environmental factors influence the implementation of the genetic program.

Since the symposium is centered around the sea lamprey, it would have been natural to concentrate on literature concerned with this species. However, very little experimental work has been performed on sexual maturation, synchony, and death after spawning in sea lampreys, so I will have to draw heavily on work done on the European river lamprey, *Lampetra fluviatilis*. Fortunately, the river lamprey has a life history very similar to that of the sea lamprey, and there is good reason to assume that knowledge gained from the river lamprey can tell us about function in the sea lamprey as well.

Upstream Migration

Only the parasitic species migrate upstream from the lakes or sea where they spend the feeding stage. At the time when migration starts, lampreys stop growing and begin to mature sexually, so only from that time is it reasonable to call them adults. The physiology of migrating lampreys was reviewed by Koch (1968), Hardisty and Potter (1971), and Fontaine (1975).

Sea lamprey (*Petromyzon marinus*) in The Great Lakes start the upstream migration in spring or early summer, 1–2 mo before spawning (Applegate 1950). A similar pattern seems to apply also to the European *P. marinus* (Fontaine 1958). The time when the European river lampreys start migration varies enormously, from late summer, about three-quarters of the year before spawning, to shortly before spawning (Zanandrea 1957; Tesch 1967). There is a tendency for the migra-

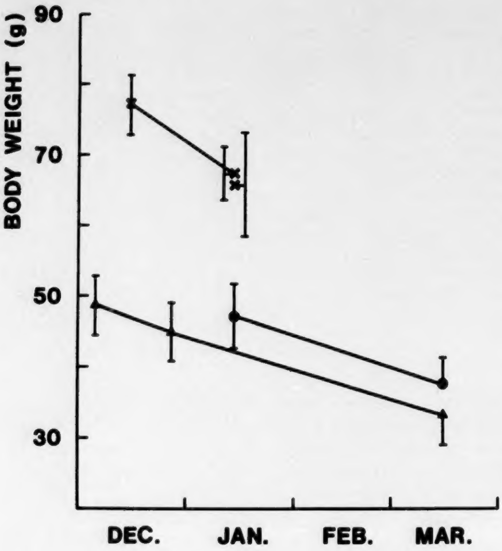

FIG. 1. Body weight of fresh run *Lampetra fluviatilis*. Data from Pickering (1970). (×) river Trent, England; (●) river Severn, England. Mean ± 2 × SE.

tion to begin earlier in northern Europe than in the south. Even within England the time of migration of river lampreys may vary from late July to March, although they probably all spawn in April or May (Abou-Seedo and Potter 1979; A. Pickering, Freshwater Biological Association, Ambleside, Cumbria, UK, personal communication).

The size of fresh run lampreys differs greatly among lampreys from different localities (Larsen 1962). Even the English river lampreys from rivers on the east coast may vary greatly in size. As shown in Fig. 1 there is a marked difference in weight of lampreys from the river Trent and the river Severn, and in both rivers early migrants weighed more than late migrants. Since the ability to osmoregulate in 33% seawater was the same in all groups, they were believed to come directly from the sea (Pickering 1970). Ivanova-Berg (1933) and Lanzing (1959) found that early (August) and late migrants (November/January) as a general rule were smaller at the time of upstream migration than those migrating in the middle of the period (September–October/October). Also, lampreys within one river system, caught at upstream migration in October or November through 16 yr, varied greatly in size (Fig. 2). The smallest and largest females were 32 g–28 cm and 116 g–42 cm, the smallest and largest males were 32 g–28 cm and 104 g–41 cm. Complicated changes in size with time were reported in a recent, extensive study of fresh run river lampreys in the estuary of Severn, England (Abou-Seedo and Potter 1979). Both in this work and in previous work by Berg (1931) and Ivanova-Berg (1933, 1936), a special small form (termed praecox) has been described. This small form may be migrating late (January to March, Abou-Seedo and Potter 1979) or at the same time as the large form (October and November, Ivanova-Berg 1933). By using the term praecox, it is suggested that these lampreys spend less time in the feeding stage at sea; however, this has not been documented.

The significance of these differences in size at the time of upstream migration is not clear. Lampreys in the phase of synchony reduce their length as well as their weight and thus maintain their proportions until spawning (Larsen 1962). Therefore the "condition factor" (the relationship between weight and length (Abou-Seedo and Potter 1979)) does not reflect the nutritional condition in the same way as in teleosts, for instance. If only weight and/or length of the migrants is known, it is impossible to evaluate what a size difference means. It is necessary to investigate parameters other than weight and length to evaluate how long lampreys have been without food. It is generally assumed that lampreys stop feeding shortly before upstream migration, and at the same time intestinal atrophy begins, leading to reduced capacity to osmoregulate in seawater (see later). From this it can be suggested that the smaller the relative size of the intestine, the longer has been the period without food. Unfortunately we have little knowledge about when feeding actually stops and how close is the correlation between intestinal atrophy, loss of marine osmoregulatory capacity, and tendency to migrate. Another problem is that we do not know for how long a time lampreys may linger at the mouth of the river before starting upstream migration (see Lanzing 1959). The difficulty in interpreting the changes seen in weight, length, and other parameters (intestine, dentition, liver, gonad) with time of capture lies in the fact that we do not know whether or not groups of lampreys migrating at various times belong to the same population. The changes in lampreys captured at upstream migration at one time of the year and kept in the laboratory (see later) may be used as a basis in these interpretations.

Nikolskii (1963, cited by Hardisty and Potter 1971) found a positive correlation between the length of migration from the sea to the spawning sites and the percentage of fat in the body at the onset of migration in various species. Whether this holds true also for early and late migrants of the same species is not known, but rather likely; the early migrants probably experience a much longer period of lack of food uptake and probably also accomplish a larger gonadal growth in this period.

The energy expenditure of migrating sea lampreys has been evaluated (Beamish et al. 1979). Calorimetry showed that the males lost $8.76\ \mathrm{J \cdot g^{-1} \cdot km^{-1}}$ (assuming a straight course) over a distance of 60 km. When they compared the cost of swimming $2.17\ \mathrm{J \cdot g^{-1} \cdot km^{-1}}$

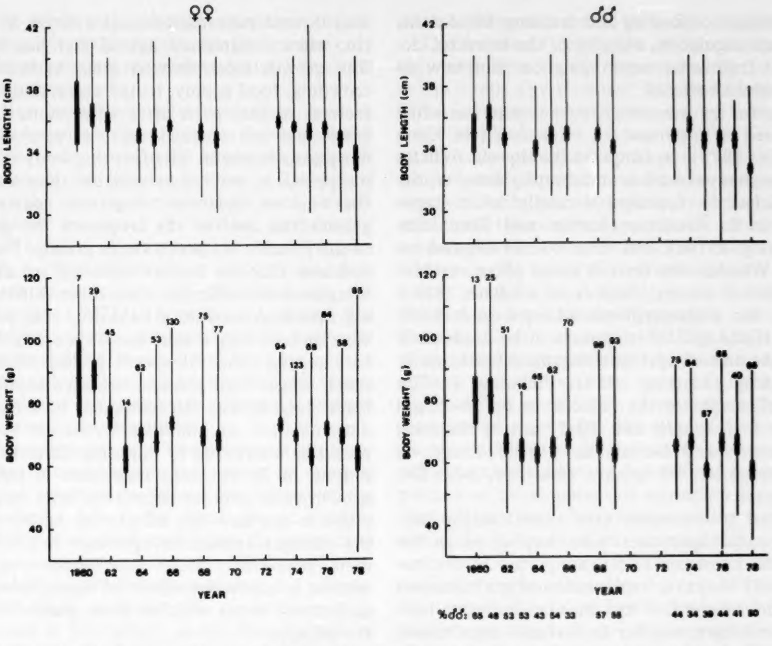

FIG. 2. Body length, body weight, and sex ratio of fresh run *Lampetra fluviatilis* from Varde river, Denmark (L. O. Larsen unpublished data). Mean ± 2 × SE; number of animals and range indicated.

with other estimates, this indicates that the lampreys do not follow a straight course.

The external factors favoring upstream migratory activity seem to be dark nights, high tide, and a certain range of temperature (Applegate 1950; Hardisty and Potter 1971; Abou-Seedo and Potter 1979).

Lampreys coming from the sea gradually lose their ability to osmoregulate in seawater and gain ability to survive in freshwater. This change involves cessation of drinking (as well as eating), the intestine undergoes atrophy, and the ion transport across the gills changes its direction (Morris 1980). But we know very little about physiological regulation of this phase of upstream migration.

Adequate osmoregulation and survival in freshwater in many teleost species require the secretion of prolactin from the pituitary gland (Nicoll 1974). In *L. fluviatilis* the pituitary gland appears to be of no great importance for osmoregulation in freshwater; survival of hypophysectomized *L. fluviatilis* in its freshwater phase is excellent (Larsen 1965).

Rapid intestinal atrophy seems to be characteristic of the early phase of upstream migration. It might be closely correlated with lack of food intake (loss of appetite?) and/or with loss of marine osmoregulatory capacity. It would be interesting to prevent lampreys from migration and keep them in seawater to see how this might affect appetite, marine osmoregulatory capacity, and intestinal atrophy. Intestinal atrophy is closely correlated with the presence of a developing gonad (Larsen 1972). Gonadectomy soon after the start of upstream migration prevents the atrophy of the intestine (Pickering 1976a), and maintains its ability to support osmoregulation in 50% seawater (Pickering and Dockray 1972). The activity of trypsin, chymotrypsin, and cholecystokinin-like substances was also followed in gonadectomized and sham-operated lampreys (Dockray and Pickering 1972). When calculated as per gram of tissue the activity did not change in any of the groups — not even in intact spawning lampreys (only trypsin tested). Substitution therapy with estradiol or testosterone implants to gonadectomized lampreys normalized the rate of atrophy, and sex hormones also increased the rate of atrophy in intact lampreys (Pickering 1976a).

This summarizes our meager experimentally based knowledge about control mechanisms during upstream migration. We really do not know what initiates the changes in behavior and physiology which are characteristic of upstream migration. I find it likely that genetic information somehow is responsible for all the mentioned changes: accumulation of a certain amount of fat, abolishment of feeding and drinking, breakdown of marine osmoregulation, atrophy of the intestine, development of freshwater osmoregulation. But how do the genes exert their effects?

In teleosts the thyrotropin–thyroid system has often been implicated as important for migration (see Koch 1968; Fontaine 1975). In lampreys the thyroid follicles produce hormones as in other vertebrates; however, the thyroid follicles do function normally after hypophysectomy in *L. fluviatilis* (Larsen and Rosenkilde 1971; Pickering 1976c) and thus do not depend on thyrotropin. Whether the thyroid gland plays any biological role is not known; there is no evidence that it is necessary for metamorphosis (Larsen and Rothwell 1972). Histologically it appears to be moderately active from the time of upstream migration until shortly before spawning (Lanzing 1959). Pickering (1972) found the cell height of the follicles to be 18–22 μm in fresh run *L. fluviatilis* and 10–17 μm in maturing lampreys. Larsen and Rosenkilde (1971) found no consistent change in ^{131}I-uptakes with time, from December to March.

The effect of gonadectomy (see above) might indicate that gonadal hormones were implicated in the atrophy of the intestine. This is supported by Pickering's finding (1976a) that implantation of sex hormones may accelerate atrophy of the intestine in intact lampreys. It is not known whether *L. fluviatilis* does secrete sex hormones at the time of intestinal atrophy; the evidence at hand is conflicting (see Hardisty 1971). Only one preliminary report on the change with time of the concentration of sex hormones in blood has appeared (Piavis et al. 1975).

The idea that a certain "critical" amount of fat (above or below a certain level) may trigger important physiological changes has appeared in the literature on teleost migration (Hoar 1976), on puberty in mammals (Kennedy and Mitra 1963; Frisch 1976), on metamorphosis in lampreys (Moore and Potter 1976), and on sexual maturation in lampreys (Larsen 1978a). The mechanism is unknown, and it is possible that the rather fixed amount of fat characteristic of a certain stage of life is the result of some special regulatory mechanism and not the cause of or signal for migration or the other processes.

One might also ask what makes the lampreys stop feeding and drinking. The two behavioral patterns are not necessarily coupled, since some species feed in freshwater where they probably do not drink. There are no experimental investigations on the central nervous structures responsible for the behavior and how they react to nervous or hormonal stimuli from the intestine and to changes in metabolite level in the blood or to changes in ion concentration or blood volume.

As mentioned, the size of lampreys at the time of upstream migration is very variable, whereas the larvae metamorphose at a rather well-defined length. It seems well documented (Manion and McLain 1971; Manion and Smith 1978) that sea lampreys metamorphose and start downstream migration at a length of about 14–15 cm, when a minimum age of 5 yr has been reached. The growth rates showed great variation related to crowding, food supply, temperature, and other external factors, so that even after 18 yr some larvae of one batch had not reached the size necessary for metamorphosis to occur. The fact that body length at metamorphosis is much less variable than body length at the time of upstream migration indicates that the growth rate and/or the length of the growth period of the juvenile lampreys varies greatly. Furthermore, it indicates that the factors initiating or allowing metamorphosis are different from those initiating or allowing upstream migratory behavior. Our present knowledge on how long a time lampreys spend feeding is not very precise, and the recent finding of larval periods much longer than hitherto expected should be remembered (see above). Development of a method for age determination in lampreys would be very useful. It would be interesting by imposing different feeding conditions, or by hormone treatment, to induce different growth rates and fat deposition rates in juvenile lampreys to see how this affects the length of time until the changes related to upstream migration ("second metamorphosis") occur. Furthermore, it might be of interest to study the effects of hypophysectomy or gonadectomy to see whether these glands are involved in the changes.

Upstream migration ends when the lampreys reach the spawning sites. It is not clear whether they show any regulated "homing" (Hardisty and Potter 1971; Tuunainen et al. 1980). If they return to their stream of origin, it does not necessarily reflect a preference, but only that they did not have to choose, because they did not go far out in the sea. Very little is known about how far lampreys migrate in the sea and how long a time they stay there; often they are caught close to the river mouth (Hardisty and Potter 1971). In Italy *L. fluviatilis* were caught 5–15 km from the coast (Zanandrea 1959), in Germany 14 km northwest of Helgoland (Bahr 1952), and in the Baltic Sea 30–40 km from the Latvian coast (E. Plisetskaya, Sechenov Institute, Academy of Science, Leningrad, USSR, personal communication).

Sexual Maturation

In lampreys sexual maturation can be defined as the period from the appearance of secondary sex characters until death after spawning. Gonadal development and its endocrine control were reviewed by Hardisty (1971, 1978) and by Dodd (1965, 1972) and by Dodd and Wiebe (1968). The sea lamprey apparently does not differ much from other lampreys with respect to gonadal development. In the investigated species the time when secondary sex characters begin to appear coincides with the time of follicle differentiation, rapid vitellogenesis, and spermiogenesis. In *L. fluviatilis*, Zanandrea (1959) found spermatozoa in a few cysts of the testis in some males shortly after their migration to the sea; but generally the testis contains only spermatogonia or primary spermatocytes until the time of sexual maturation.

Secondary sex characters differ somewhat between species. In sea lampreys the males develop a ropelike ridge along the back, and in the branchial region it becomes distended; the females develop a fleshy keel ventrally, from the anus to the caudal fin, and a thickening of the lower margin of the tail fin; furthermore the body swells because of growth of the ovary (Applegate 1950). In *L. fluviatilis* the time sequence and rate of development of secondary sex characters was described by Larsen (1973); in males the dorsal fins increase in height and the urogenital papilla grows; in females the second dorsal fin swells at the base and an anal fold develops; in both sexes the cloacal region swells. In *L. planeri* the secondary sex characters are very similar to those of *L. fluviatilis*.

Essential for spawning and fertilization is the urogenital papilla through which the sperm is released close to the eggs as these are being stripped out of the female by the male. I have not been able to confirm Knowles' (1939) often-cited report that the connection between the body cavity and the urogenital papilla becomes established shortly before spawning in *L. fluviatilis*. In Danish river lampreys this connection is established already in November; at this time granulated carbon injected into the body cavity may be pressed out through the urogenital papilla in both males and females (unpublished data). The anatomical arrangement is well described by Marinelli and Strenger (1954, fig. 47). The swelling of the cloacal region before spawning is partially explained by infusion of blood (Knowles 1939), but growth of the muscle surrounding the base of the urogenital papilla also contributes (Larsen 1974). Furthermore fat is accumulated in the skin of the cloacal region (unpublished data).

Spawning behavior does not take place under ordinary laboratory conditions, because flowing water and presence of gravel are necessary conditions (see Hagelin 1959). No experimental investigations have been published on the control mechanisms behind the change in daily locomotor activity before spawning (Sjöberg 1977), which seems to be related to an apparent lack of photophobia or even preference for light (Sterba 1952), or behind spawning behavior itself.

An experimental investigation of the effect of external factors on sexual maturation was performed on *L. fluviatilis* (Larsen 1973). Sexual maturation progressed normally even if the lampreys were kept in darkness from time of capture in autumn. When the temperature was kept constantly low (~6°C) maturation was late and not well synchronized. At a constant high temperature (~11°C) it was early and well synchronized. Later experiments have shown that lampreys also mature normally when kept in darkness and at constant temperature at the same time. The findings agree well with observations under more natural conditions (Plisetskaya et al. 1976; Sjöberg 1977).

The hormonal regulation of sexual maturation has only been investigated experimentally in *L. fluviatilis* in the 1960s (by Evennett and Dodd and by Larsen). These investigations are reviewed by Larsen and Rothwell (1972) and by Larsen (1973). Further experiments were published by Larsen (1974). The experiments involved partial and total hypophysectomy, substitution with gonadotropins, transplantation of the pro- and meso-adenohypophysis, gonadectomy, and treatment with sex hormones. The results show a picture similar to the general vertebrate picture in most respects: sexual maturation depends on the presence of the pro- and meso-adenohypophysis, corresponding to the pars distalis of tetrapods. The site of production of the putative gonadotropin(s) is still under discussion, and no gonadotropin has been extracted, isolated, or characterized chemically. Treatment with mammalian gonadotropin or with extracts of lamprey pituitary glands tended to normalize sexual maturation in hypophysectomized lampreys, but did not induce a clear-cut precocious development of secondary sex characters in intact lampreys. Substitution with testosterone or estradiol-17_β normalizes development of secondary sex characters in gonadectomized lampreys, but does not induce precocious development in intact lampreys. Contrary to other vertebrates the heterotopically transplanted pro- and meso-adenohypophysial tissue may allow sexual maturation to occur, including spermiation and ovulation. The importance of gonadotropin stimulation is not so marked; after hypophysectomy vitellogenesis may continue at a low rate, and no atrophy of the gonads takes place even after many months. If hypophysectomy is performed shortly before expected ovulation, ovulation may occur up to 2 wk after the operation, indicating that a gonadotropin surge is not necessary for ovulation. There is no conclusive physiological evidence of feedback from the gonad on the pituitary gland (Larsen 1974).

The pineal is often thought to be involved in regulation of gonadal function. Pinealectomy retards sexual maturation in male and female river lampreys (Joss 1973); however, daily injection of melatonin, a substance from the pineal assumed to be a hormone, also has this effect (Eddy 1972). Perhaps in both cases the effect on sexual maturation was caused by a general disturbance of the metabolism of the lampreys.

One important metabolic process behind sexual maturation in females is vitellogenesis. Pickering (1976b) showed that estrogen implants increased the yolk protein content of the blood and the dry weight of oocytes and caused liver hypertrophy in *L. fluviatilis*. Extirpation of the liver abolished the rapid phase of vitellogenesis (Larsen 1978b). These experiments support the generally accepted idea that precursors of yolk are produced in the liver under influence of estrogen and taken up by pinocytosis in the ovary under the influence of gonadotropin.

The pituitary gland is necessary not only for growth of the oocytes, but also for the differentiation in the ovarian follicle necessary for ovulation and for the survival of the released oocyte and its fertilization. This differentiation involves formation of acid and neutral mucopolysaccharides (Larsen 1970). I suggested that swelling of mucopolysaccharides plays a role in the rupture of the follicle at ovulation and in the release of the oocyte from the ovary. Mucopolysaccharides moreover are present in the "tuft" through which the spermatozoa enter the zona pellucida (Kille 1960) and in the sticky layer which makes the egg adhere to sand in the nest (Busson-Mabillot 1967, a, b). The chemical nature of the tuft and of the sticky layer has recently been described (Yorke and McMillan 1979). Mucopolysaccharides in the cortical granules are responsible for the formation of a perivitelline space at fertilization (Yamamoto 1944).

Processes Associated with Synchony

It may be wise to avoid using the term starvation for the final phase in the lamprey's life, because this word indicates a stressful situation in which the animal is prevented from obtaining food. In the case of the parasitic lampreys, food remains available and the lack of feeding is probably a "programmed" and regulated behavioral phenomenon. In the nonparasitic lampreys, feeding behavior never develops after metamorphosis.

The phase of synchony is characterized by mobilization of lipid and protein reserves which were accumulated during larval growth in nonparasitic species and during the juvenile feeding stage in parasitic species. The protein is mainly drawn from the muscles and the lipid from several organs (see later).

The following review will describe the time sequence of gross changes in morphology and the associated biochemical changes as quantitatively as possible and summarize what is known about regulatory mechanisms.

GROSS CHANGES

The gross morphological changes taking place from the time of upstream migration until spawning have been described thoroughly in both sea and river lampreys, because at these two stages the lampreys are easy to catch. A study of the rates of the changes and their regulation necessitates supplementary studies, where the time course of the events can be followed. Such studies on *L. fluviatilis* are reported by Larsen (1973), and a summary will be given below. *Lampetra fluviatilis* is especially interesting, because it has such a long phase of synchony, in Danish lampreys starting about 4 mo before sexual maturation is initiated and altogether lasting about 7 mo. In principle the changes seem to be very similar in sea lampreys. I will specify differences when they are known.

Body weight of *L. fluviatilis* declines gradually from autumn until shortly before spermiation and ovulation at which time the weight of females increases because of water uptake. The weight decreases at spawning in both sexes because of loss of gonadal products.

Body length shows a slow reduction in autumn and early winter; and a rapid reduction, most marked in females, takes place from the time when secondary sex characters begin to develop and continues until natural death. A comparable, but more compressed time course in reduction in length of *P. marinus* was recently described by Potter and Beamish (1977).

The *body wall* (the body after removal of the head, the gill region, and all organs in the body cavity), i.e. mainly skin and muscle, shows a reduction in weight parallel with the reduction in length of the body; the rate of reduction in body length thus seems to reflect the rate at which tissue of the body wall is mobilized to cover energy requirements and to build up gonads. The energy requirements appear to rise at the time of sexual maturation as revealed by the increase in oxygen uptake (Claridge and Potter 1975) and in the increase in ventilation rate and rate of heart beat (Lewis 1980).

The *testis* increases in weight from ~3 to ~7% of the initial body weight, the maximum size being reached at the time when spermiogenesis starts. The *ovary* increases from ~6 to ~16% with a slow rate of growth until secondary sex characters begin to develop and a rapid growth from then until ovulation.

The total change in weight of the body wall is from ~65 to 45% of the initial body weight in females, and this shows that the body wall contains mobilizable material enough for ovarian growth. Investigations on the sea lamprey have shown a dramatic reduction in thickness of the body wall (apart from its shortening in length) and a marked reduction in the size of the lipid layer in the dermis (Anderson and Manion 1977).

The weight changes in the liver and intestine are of such small absolute values that they play no important role in the overall balance sheet. The *liver weight* in males is reduced for some months, from ~1.2 to 0.8% of the initial body weight, and increases again at sexual maturation, reaching about 1.9%. In females the liver initially is a little larger than in males, and it decreases gradually in weight until death, from ~1.7 to ~0.8%. The different time course of the liver weight changes in males and females led Kott (1970) to the suggestion that there are genetic differences between two populations of sea lampreys; however, the differences rather reflect their different stage in sexual maturation (one population was migrating, the other had spawned). The *intestine* undergoes a rapid atrophy during the first 3 mo (from a diameter of about 3 mm to about 1 mm), and when secondary sex characters begin to develop it does not atrophy further. The atrophy is reflected in a reduction in diameter and weight and in atrophy of the epithelium and disappearance of the folds. The reduction probably has begun when the lampreys are still in the sea, when the diameter may exceed 10 mm; the earliest fresh run river lampreys have diameters of 7–8 mm (Lanzing 1959).

Parallel with the atrophy of the intestine, the *horny teeth*, which are long and pointed during the feeding stage and at upstream migration, become short and blunt; the changes are stepwise, because the horncaps are shed at intervals of a few weeks. The changes in dentition of the sea lamprey have been described by Vladykov and Mukerji (1961) and by Manion and Piavis (1977). In sea lampreys the change in size and form is not so marked as in the river lamprey, but the teeth of spawning lampreys appear "worn out" or "degenerated."

The *heart* is the only investigated organ that does not change its weight during the whole freshwater phase — probably the kidneys do not either, since both organs are basic for survival. The unchanged absolute weight of the heart really means that its relative size increases with time.

A noticeable change in the *color of the blood and liver* occurs at sexual maturation. The blood becomes pale, and the erythrocytes degenerate and disintegrate. At the same time the liver becomes green in 33–91% of the river lampreys, more often in males than in females; the variation is great from year to year. In *P. marinus* all livers become green, dark green in females and light green in males (Applegate 1950). The drop in hematocrit is less dramatic in *P. marinus* than in *L. fluviatilis* (Potter and Beamish 1978) indicating that disintegration of erythrocytes is not so marked and/or that formation of new erythrocytes keeps better pace with it. In *P. marinus* the skin turns yellow, and the yellow pigment may be rubbed off (Kott 1973). The same phenomenon can occasionally be observed in the river lamprey (own unpublished observations). The green and yellow pigments are probably bile pigments formed by degradation of hemoglobin from the disintegrated erythrocytes and deposited in the liver or excreted by the skin (and probably by the kidney and intestine as well, since the green substance (biliverdin) may be accumulated in these two organs — see Morris' observation cited in Larsen and Rothwell 1972, p. 51). The normal way of secretion of bile pigments via the bile bladder does not occur any longer, because the bladder and duct undergo atrophy before sexual maturation as do the portal vessels. The atrophic changes in the liver have been described by Minelli and Rossini (1961), Bertolini (1965), and by de Vos et al. (1973).

The gross changes in the various *organic fractions* have also been investigated, but the data are still incomplete. In Table 1 I have summarized the most important data from *L. fluviatilis* and *P. marinus* to try to get an overall picture of how energy requirements are covered in the phase of synchony and the source of material used for gonadal growth. For this purpose it is necessary not only to know concentrations of carbohydrates, protein, lipid, etc., but also to know the total content in the whole body and in various organs; this necessitates knowledge of organ weight. This is unfortunately not easy to determine for musculature which is by far the largest organ of the body of the fresh run lamprey.

Table 1 shows the data for lipid concentrations. Lipid is stored in other organs, e.g. in the central nervous system (Müller 1968), in the supraneural organ (George and Beamish 1974; Kelényi and Larsen 1976; Potter et al. 1978), and in the skin (Anderson and Manion 1977). In juvenile lampreys there is also fat accumulation in the kidneys (Weissenberg 1927; fig. 2 and 4 in Applegate and Thomas 1965). It is possible from the data in Beamish et al. (1979) to estimate the size of these extra fat deposits in *P. marinus*, which seem to add up to a considerable amount (Table 2).

In a few cases the time course of changes from start of upstream migration until death after spawning has been followed. Beamish et al. (1979) analyzed a large number of freshly caught anadromous sea lampreys at early migration, when nearly mature, spawning, and spent, and they also investigated small and large feeding juvenile lampreys. Similar but not so extensive data were collected from river lampreys by Tilik (1932) and by Moore and Potter (1976). The changes with time in the laboratory under controlled conditions were investigated by Larsen (1973) (only organ weights) and by Oakley et al. (1979) (Table 3). In this study the changes of histochemical reactions were also recorded for muscle tissue of the body wall. Glycogen, as demonstrated by a positive PAS-reaction, was equally distributed in the various types of muscle fibers. The body wall musculature can be divided in a central or inner and a parietal or outer portion, with a preponderance of myosin ATPase-positive fibers in the central layer and myosin ATPase-negative fibers in the parietal layer (see Rovainen 1980). Fat, as demonstrated by Sudan B, was present in October both in the myosin ATPase-negative and the myosin ATPase-positive fibers, but in January only the myosin ATPase-negative fibers contained fat. In March the myosin ATPase-negative fibers appeared partially depleted. There was no obvious change in thickness of muscle fibers with time. When discussing "muscle" in lampreys, it is important to distinguish between muscles of the body wall and that of the suctorial apparatus (see Table 3); these two types also differ in their response to insulin; only the suctorial apparatus responds to insulin by glycogen synthesis (Leibson and Plisetskaya 1968). Oakley et al. (1979) investigated both dorsal and ventral parts of the muscle in the body wall and found very small differences; Beamish et al. (1979) investigated the lateral parts in the anterior, middle, and posterior part of the body and did not find any great differences either.

Whereas the data of different authors for lampreys at the start of upstream migration are rather similar, they differ widely with respect to the final stages. At the

TABLE 1. Survey of body constituents in fresh run lampreys (body

	Organ weights in % of body weight		Water content, % f.w.		Carbohydrates, % f.w.
	L. fluviatilis	*P. marinus* (anadromous)	*L. fluviatilis*	*P. marinus* (anadromous)	*L. fluviatilis*
Total body			♂+♀ 66–77[10,5,6]	♂ 76[1] ♀ 72 (calculated)	
Body wall (see text)	♂ 69 (66 g)[7] ♀ 67 (76 g)[7]				
Musculature	♂+♀ 70[8]			♂+♀ 72[1] (carcass, – skin and internal organs)	♂+♀ 0.245[2] ♂+♀ 0.425–0.500[9] (not defined, probably from body wall)
Gonad	♂ 3.5[7] ♀ 5[7]	♂ 2.15 (876 g)[1] ♀ 11.16 (896 g)[1]		♂ 84[1] ♀ 57[1]	
Liver	♂ 1.2[7] ♀ 1.7[7]	♂ 2.07[1] ♀ 1.98[1]		♂ 61[1] ♀ 75[1]	♂+♀ 0.126[2] ♂+♀ 0.050–0.250[9]
Heart	♂+♀ 0.3[7]				
Kidneys	♂ 0.49±0.02[a] (54 g)[13] ♀ 0.34±0.02[a] (60 g)[13]				♂+♀ 0.3[12]
Brain	♂+♀ 0.040 (71 g)[4]				♂+♀ 2[9] ♂+♀ 1[12]
Intestine	♂+♀ 1 (104–108 g)[6]				
Extracellular fluid			♂+♀ 22[11]		♂+♀ 0.020–0.030[8]
Blood					

[a] Kidney weights at natural death in percentage of initial body weight (November) 21 ♂♂ versus 21 ♀♀: $P < 0.001$. Natochin, (1972) found a value of 0.55% in male and female *L. fluviatilis* in winter.

REFERENCES: [1]Beamish et al. 1979; [2]Bentley and Follett 1965a; [3]Bentley and Follett 1965b; [4]M., Bundgård, Department of Physiology, Panum Institute, University of Copenhagen, Denmark, personal communication; [5]Hardisty 1956; [6]Lanzing 1959; [7]Larsen 1973;

time of *spawning* the changes are so rapid that it becomes very important to define exactly the stage of development of secondary sex characters and of the gonad. Also the motor activity may influence especially the glycogen levels very much, so it is important to know whether or not the animals have been engaged in nest building and spawning activity. Muscle glycogen seems mainly to be spared for the motor activity during spawning, a conclusion also reached by Plisetskaya et al. (1976).

It seems reasonably safe to conclude on the basis of the data reported by Beamish et al. (1979) and by Moore and Potter (1976) that protein and lipid are used for energy requirements to the same extent in the whole phase of synchony, with a slow phase of mobilization in the beginning and a rapid phase during spawning. This rapid phase is also seen in laboratory lampreys not showing nest building or spawning, as reflected by the increased rate of reduction in length (Larsen 1973).

From the data obtained by calorimetry (Beamish et al. 1979) I have calculated that the sea lamprey males and females, with initial mean body weights of 876 and 896 g, lost about 2720 and 4190 kJ from the time of upstream migration until they had spawned (about 50 d). The data for lipid and protein show that males and females used 59 and 52 g lipid in this period, whereas the use of protein was much higher in females (58 g) than in males (18 g) because of the great loss of protein with the eggs (all eggs ovulated corresponds to a loss of 37 g protein). The amount of protein transferred to the ovary from the rest of the body from upstream migration until maximal development of the ovary was 16 g. Beamish (1979) calculated energy metabolism. During migration, males and females spent at most 1320 and 1090 kJ, respectively, in locomotion, and during spawning, 1850 and 1760 kJ, respectively, in nest construction and spawning behavior.

In the river lamprey, calculations by Moore and Potter (1976) show that the lipid content in the ovary of early migrants was 0.86 g and at sexual maturity 1.94 g. The total amount of lipid in the body was weight in parentheses; f.w. = fresh weight; d.w. = dry weight).

Carbohydrates, % f.w.		Protein, % f.w.		Lipid	
Absolute amount in 100 g *L. fluviatilis*	*P. marinus* (anadromous)	*L. fluviatilis*	*P. marinus* (anadromous)	*L. fluviatilis*	*P. marinus* (anadromous)
		♂ 11.5[16] ♀ 11.8[16]	♂ 13[1] ♀ 16 (calculated)	♂+♀ 7–18% f.w.[16,6,3,10]	♂ 10% f.w.[1] ♀ 11% f.w. (calculated)
(240 mg)	♂ 0.298[1] ♂ 0.352[1] (lateral region of trunk − skin)		♂+♀ 17[1] (carcass, − skin and internal organs)	♂+♀ 40% d.w.[3] ♂+♀ 18% f.w.[10] (body, − liver and gonad)	♂+♀ 8% f.w.[1] (carcass, − skin and internal organs)
	♂ 0.037[1] ♀ 0.346 (nearly mature)		♂ 12 ♀ 23	♂ 8% f.w.[10] ♀ 17% f.w.[10]	♂ 2% f.w.[1] ♀ 14% f.w.[1]
(1 mg)	♂ 0.028[1] ♀ 0.052[1]		♂ 12 ♀ 16	♂+♀ 45% d.w.[3] ♂ 23% f.w.[10] ♀ 14% f.w.[10]	♂ 21% f.w.[1] ♀ 4% f.w.[1]
(<1 mg)					
(<1 mg)					
(6 mg)					
		♂ 5.3[14] ♀ 5.2[14]		♂ 0.88 μeq/mL[15] } free fatty ♀ 1.02 μeq/mL[15] } acids	

[8] Larsen 1976a; [9] Leibson and Plisetskaya 1968; [10] Moore and Potter 1976; [11] Morris 1972; [12] Murat et al. 1979; [13] A. Olsen, Zoophysiological Laboratory A, University of Copenhagen, Denmark, personal communication; [14] A. Pickering, personal communication; [15] Plisetskaya and Mazina 1969; [16] Tilik 1932.

9.25 g in males and 9.54 g in females of early migrants, 2.5 and 4.7 g at maturity, and 1.36 and 1.14 g after spawning.

The considerations of how the energy expenditure is covered by the various organic fractions may be supplemented by a calculation relating the loss of energy to oxygen consumption. Rate of oxygen consumption varies from 0.01 to 0.11 $mL \cdot g^{-1} \cdot h^{-1}$ in adults of various lamprey species, dependent on temperature, for instance (see Claridge and Potter 1975). If the loss of 2720 kJ in the 876-g *P. marinus* males (who lose only a small amount of gonadal products) are converted into oxygen equivalents (assuming that 4.2 kJ = 4.8 L oxygen) their rate of oxygen consumption in the period of 50 d should be 0.1 $mL \cdot g^{-1} \cdot h^{-1}$ (i.e. a very reasonable figure).

REGULATION OF GROSS CHANGES

Hormones probably play a role in mobilization of protein and lipid during the phase of synchony, but their role may well be modest; they only permit or stimulate rates of processes that occur also in the absence of hormones.

There is no evidence for a special lipid-mobilizing hormone from the pituitary gland. Corticosteroids, which are generally assumed to be involved in mobilization of protein and the transformation of amino acids to glucose (gluconeogenesis), have not been demonstrated in adult lampreys (Buus and Larsen 1975), although some steroidogenic activity is present in the presumptive adrenocortical pronephric tissue (Weisbart et al. 1978). However, there is evidence of the presence of corticotropin in the pituitary gland (Larsen and Rothwell 1972), and corticotropin has direct metabolic effects on muscle tissue in a mammal (Bassett et al. 1978). The presence of glucagon ("the hormone of hunger") has been considered doubtful because of lack of α-cells in the pancreatic islets and because of lack of hyperglycemic effect of mammalian glucagon (Larsen 1976b; Brinn and Epple 1976).

TABLE 2. Lipid in fresh run *Petromyzon marinus* (anadromous). (Data (weight in grams) calculated on basis of Beamish et al. 1979).

	♂♂	♀♀
(Total body weight	876 g	896 g)
Musculature	49	50
Liver	4	0.7
Gonad	0.4	14
Sum	53	65
Total body	89	99
Other sites	36	34

It is also possible that the mobilization of the body wall, which increases in rate at the time of sexual maturation, is secondary to gonadal growth and differentiation or depends on sex hormones acting peripherally. It should be possible to test whether pituitary hormones different from gonadotropin are responsible for the processes associated with synchony by comparing the effects of hypophysectomy and gonadectomy. After both operations the rate of mobilization of the body wall and the reduction in length of the body are slowed down in those lampreys that survive for a reasonable period (Larsen 1973). The only normal change during synchony, which does not take place in hypophysectomized lampreys but may do so eventually in gonadectomized lampreys, is the green coloration of the liver. This indicated that except for the green coloration of the liver all the processes related to synchony are also closely related to gonadal development and possibly caused by sex hormones. The degenerative changes in the intestine, which occur before sexual maturation, are slowed down a little by hypophysectomy in autumn. As mentioned, they are also prevented or even turned to a transitory hypertrophy after gonadectomy in autumn. When gonadectomy is performed in January, shortly before sexual maturation is initiated, a marked increase in diameter of the intestine takes place, and the atrophied epithelium shows redifferentiation and development of folds (Larsen 1972, 1973). This hypertrophy does not depend on a factor from the pituitary gland (Larsen 1973), and it is not counteracted by treatment with sex hormones (Larsen 1974; Pickering 1976a). This is surprising, since, as mentioned, treatment with sex hormones in autumn caused atrophy in gonadectomized lampreys. This may indicate that some unknown factor in the gonadectomized January-lampreys counteracted the atrophy-inducing effect of the sex hormones or that the intestine had lost its sensitivity towards sex hormones at this time of the year. The only safe conclusion at the moment is that normal atrophy of the intestine in some way is correlated with the presence of a developing gonad, and when the gonad is removed the intestine undergoes a transitory hypertrophy which seems inde-

TABLE 3. Water and organic fractions during the phase of synchony in *Lampetra fluviatilis*[a] (mean, range, and number of lampreys) (f.w. = fresh weight) Oakley et al. (1980).

	Batch	Sex	Water %	Triglycerides mmol/kg f.w.	Glycogen mmol glucose/kg f.w.	Protein mg/g f.w.
Muscle in body wall	Oct.	♂+♀	66.8 (64.3–68.1) 6	156 (106–248) 4	4.8[b] (2.1–8.2) 6	19.1 (16.4–22.3) 4
	Jan.	♂+♀	71.7 (69.1–72.9) 6	108 (72–146) 4	14.1 (11.1–18.8) 6	
	Mar.	♂+♀	76.2 (73.9–80.1) 6	76 (31–94) 4	17.2 (8–21.0) 6	13.8 (13.3–14.3) 4
	Spent	♂+♀	84.7 (83.0–85.9) 3	18 (13–22) 3	4.7 (1–6) 3	11.9 (9–14) 3
Muscle in suctorial apparatus	Oct.	♂+♀	75.6 (73.2–78.2) 4	16 (11–19) 4	13.3 (11.1–14.4) 6	
	Jan.	♂+♀			21.7 (18.1–24.6) 6	
	Mar.	♂+♀	83.0 (78.0–84.9) 6	11 (8–13) 4	23.8 (20–30) 6	
Heart	Oct.	♂+♀	75.8 (74.0–77.2) 3	45 (28–54) 4	17.3 (6.1–38.2) 4	
	Jan.	♂+♀		47 (39–51) 4		
	Mar.	♂+♀	82.8 (82.1–83.4) 4	42 (38–44) 4	14.7 (11.1–21.4) 4	
Liver	Oct.	♂	66.1 (64.2–67.3) 3	95 (89–101) 2	4.3 (3.8–5.5) 3	
		♀	67.2 (66.0–67.8) 3	72 (68–76) 2	3.3 (3.2–3.3) 3	
	Jan.	♂		84 (76–92) 2	7.5 (5.2–9.8) 3	
		♀		37 (35–39) 2	6.1 (5.4–6.5) 3	
	Mar.	♂	73.1 (72.8–73.5) 3	17 (16–17) 2	3.6 (3.4–4.0) 3	
		♀	79.4 (78.8–79.9) 3	6 (4–8) 2	3.9 (3.4–4.2) 3	
	Spent	♂+♀	78.3 (74.0–81.2) 3	8 (3–21) 3	19 (14–28) 3	

[a] River lampreys were caught in Varde river, Jutland, during upstream migration and kept in the laboratory at 11°C. In March they were fully sexually mature. Spent river lampreys were obtained from Rickle river, Northern Sweden, through the courtesy of Dr. Kjell Sjöberg. Biopsies were subjected to micromethods (triglycerides, Essén et al. 1975; glycogen, Karlsson et al. 1970; protein, Lowry et al. 1951).

[b] This low value probably reflects that this batch of lampreys were moving restlessly before decapitation.

pendent of hormones from the pro- and meso-adenohypophysis. The atrophy seems not to be a simple consequence of lack of food uptake, since hypertrophy can take place after several months of synchony.

The transformation of the teeth from long and pointed to blunt and short are not consistently affected by either hypophysectomy or gonadectomy (Larsen 1973).

INTERMEDIARY METABOLISM

To understand the physiology of the lampreys during synchony it is important to know as much as possible about the metabolism of protein, lipid, and carbohydrate. Recently an interesting report on intermediary metabolism in larvae and metamorphosing stages of *P. marinus* appeared (O'Boyle and Beamish 1977).

In adult lampreys very little is known about protein and lipid metabolism, whereas carbohydrate metabolism has attracted more interest (or rather, the methods are more easily available). Blood glucose is circulating and deposited as glycogen in liver, muscle, brain, and kidneys (Leibson and Plisetskaya 1968; Murat et al. 1979). The glycogen may be broken down again to glucose and liberated to the blood from the liver and the kidneys which contain the necessary enzymes (Murat et al. 1979). In the brain it seems that the meninges are able to break down glycogen and release glucose to the nervous tissue, at least in larvae (see Rovainen et al. 1971). According to the general vertebrate pattern muscle glycogen is broken down to carbon dioxide or lactic acid, which in the liver can be transformed to glucose. This probably also takes place in lampreys, because in the Australian lamprey, *Mordacia mordax*, liver slices do produce glucose from lactate (Phillips and Hird 1977a). Glucose may also be formed from certain amino acids originating from breakdown of muscle protein, or from glycerol being released from the fat cells on fat mobilization. This gluconeogenesis would be expected to take place in the liver, but at the moment we have only negative evidence; the liver of *M. mordax* does not form ketone bodies from butyrate (Phillips and Hird 1977b). The lamprey liver seems to lack a number of functions found in higher vertebrates (Is lack of detoxification the reason that ammocoetes are specially sensitive towards TFM?) (see Larsen 1978b). In the sliced muscles of *L. fluviatilis* added labeled glycerol can be incorporated into glycogen (Savina and Plisetskaya 1976; Savina and Wojtczak 1977), indicating that the lamprey muscle is able to perform at least the short pathway of gluconeogenesis. Little is known about gluconeogenesis based on protein breakdown (Savina and Wojtczak 1977). It is possible that the kidneys of lampreys, as in mammals after prolonged starvation, are able to perform a considerable gluconeogenesis; at least its activity of glucose-6-phosphatase is high compared with that of the liver and the brain (Murat et al. 1979).

Blood glucose levels do not decrease in spite of prolonged lack of food uptake, indicating that gluconeogenesis takes place during the whole phase of synchony. The blood glucose levels are constant from upstream migration and even rise at the time of ovulation and spermiation, and this seems to be a well-regulated phenomenon (Larsen 1976a). It possibly reflects the high activity in all metabolic processes of the lamprey in this phase, including gluconeogenesis as suggested by Plisetskaya et al. (1976).

The metabolism of lipid has not been investigated; all that is known is that free fatty acids are circulating (Plisetskaya and Mazina 1969).

Protein metabolism is also nearly unknown; nitrogen is mainly excreted as ammonia (Read 1968).

It is not known which substrates provide energy in the various tissues. Since the brain contains large glycogen stores, it may depend exclusively on carbohydrates, but on the other hand an organism which for a long time has to live mainly on its stores of lipid (and protein) might be expected to be able to oxidize glycerol, fatty acid, and ketone bodies (and amino acids) both in the brain and elsewhere. Such abilities might explain why insulin-treated lampreys show a remarkable ability to survive and move normally for several days even with blood glucose levels below the detection level (measured by the very sensitive hexokinase method (Larsen 1976a)).

There is a need for investigations of turnover of various metabolites to get a clearer picture of the dynamics and quantitative relations in metabolism. Larsen (1976a) found evidence that glucose turnover is increased at the time of ovulation and spermiation, since endogenous (stress-induced) or exogenous glucose loads were removed from the blood more rapidly than before.

REGULATION OF METABOLISM

Our knowledge of insulin, one of the key hormones in metabolism, is well advanced as a result of extensive work done by Leibson, Plisetskaya, and their co-workers on river lampreys (Plisetskaya et al. 1976; Leibson et al. 1976). The role of insulin in carbohydrate metabolism has been most thoroughly investigated and seems to be similar to that in mammals, although the responses are very slow. Because adult lampreys live on blood, flesh, and fat, either that of other fish or their own, protein and fat metabolism are quantitatively very important; in this respect it is interesting to note that insulin release in response to lysine and arginine is larger and more rapid than in response to glucose (Plisetskaya et al. 1976). There is also evidence that insulin is of importance in fat metabolism. Injection of insulin caused a distinct and prolonged lowering of free fatty acids in blood plasma (Plisetskaya and Mazina 1969), and anti-insulin serum caused an increase (J. C. Murat, Laboratoire de Physiologie, Université Paul Sabatier, Toulouse, France, and E. Plisetskaya, personal communication).

Insulin levels (relative values obtained by radioimmunoassay) in blood during synchony show an interesting pattern. In the period from October to December there was a slow decrease from 30 to 25 μU/mL. From December the decrease was rapid, reaching values of 5 μU/mL in February. Then there was some increase to 10–13 μU/mL in March to May, just before spawning. At spawning and just before natural death the values were 2–3 μU/mL. In another series of experiments it was revealed that the insulin levels were not higher in marine lampreys than in animals caught in the river mouth; lampreys at sea and actively feeding contained 0.96 ± 0.06 ng/mL; lampreys at sea and not feeding 1.1 ± 0.06 ng/mL; and when entering the river mouth, 1.4 ± 0.09 ng/mL (Polyakova and Plisetskaya 1977) (1 ng corresponds to 20–25 μU, see Plisetskaya et al. 1976). According to histological investigations the pancreatic islet tissue was most active during the marine period and before spawning (Polyakova and Plisetskaya 1977). To get an understanding of the biological significance of these data, it would be interesting to know whether the biological half-life of insulin changes during the life cycle and whether sensitivity to insulin changes. In the phase of synchony the most important function of insulin may be a negative one: its lowered secretion may allow increased rate of mobilization (not counteracting the catabolic processes in the liver, muscles, and fat stores). It would be highly interesting to know what causes the changes in insulin levels before and during sexual maturation.

It is reasonable to assume that insulin plays a more essential role in the growth phase, since insulin is generally found to be important for anabolic processes. The slow response of insulin secretion (Plisetskaya et al. 1976) to changes in metabolite concentrations (several hours) may reflect that lampreys are rather continuous feeders as larvae and at least have long-lasting meals in the parasitic phase. In phylogenetic development, this way of feeding was probably also correlated with their lack of a stomach.

Adrenalin increases the levels of both glucose and free fatty acids in the blood (Plisetskaya and Mazina 1969). Also various types of stress cause a rise in blood glucose (Larsen 1976a), probably acting via catecholamine release (Stabrowsky 1967; Mazeaud 1969). How stress affects catecholamine release is unknown. There is no evidence that the catecholamine-producing cells in the heart are innervated (Beringer and Hadek 1972; Govyrin 1967; Smitten 1972). The blood glucose rises after stress even in nearly totally hepatectomized lampreys (Larsen 1978b). This may suggest an increased production of glucose somewhere else, but could perhaps also be due to decreased utilization of glucose in muscles. In this respect it is of interest that adrenalin inhibits insulin secretion when the insulin levels are high (Plisetskaya et al. 1976), and that the most important function of insulin in carbohydrate metabolism seems to be its effect on uptake of glucose in muscles (see discussion by Larsen 1978b). If stress inhibits insulin secretion and thus increases blood sugar levels, it probably acts via adrenalin released to the blood, because the pancreatic tissue of lampreys is not innervated (Epple and Brinn 1975; Brinn and Epple 1976).

Recently John et al. (1977) found some evidence for an "adipokinetic" effect of vasotocin; vasotocin partially counteracted the fall in free fatty acid levels in blood seen in saline-injected lampreys. If an adipokinetic effect of vasotocin can be confirmed, it will be important to compare the effect of total hypophysectomy with that of extirpation of the pro- and meso-adenohypophysis in studies of the phase of synchony.

In general very little is known about the autonomic nervous system in lampreys and its role in intermediary metabolism; its possible effects in mobilization of metabolites during synchony is totally unknown. Govyrin and Popova (1965) found that adrenergic structures in the adipose tissue of *L. fluviatilis* did not innervate the adipose tissue directly. Possibly the metabolism of lampreys depends more on regulatory systems directly related to metabolite concentrations and do not depend so heavily on either hormones or nerves as does the metabolism of higher vertebrates.

Death after Spawning

As mentioned earlier, all lamprey species are stated to die soon after their first and only spawning; they also die if they are prevented from actual spawning (Applegate and Smith 1950; Larsen 1973) and kept free of fungus infections (Larsen 1973). In phylogenetical development death after spawning has probably been associated with the lack of oogonia or spermatogonia in sexually mature lampreys. Before or during sexual maturation all oogonia or spermatogonia are in a synchronous way transformed to oocytes and spermatozoa, and thus there is no basis for further reproduction. The catabolic processes of synchony must lead to death sooner or later. There are, however, indications in the literature that some individuals, especially *P. marinus*, may survive several months after spawning (Fontaine 1958).

Only in river lampreys have the causes of natural death been studied experimentally (Larsen 1973, 1974). The conclusion of this work is that when sexual maturation is abolished by hypophysectomy or gonadectomy or delayed by low temperature, natural death is delayed. In hypophysectomized lampreys the delay may be for up to 13 mo, and in gonadectomized for up to 4 mo. In *P. marinus* kept at 5°C, sexually mature males and females survived for up to 9 mo after the normal time of spawning (J. Teeter, Monell Chemical Senses Center, University of Pennsylvania, Philadelphia, PA, USA, personal communication). In some river lamprey males with partial hypophysectomy or autotransplanted pro- and meso-adenohypophysial tissue, normal sexual maturation, including spermiation, took place, but they did show prolonged survival. This suggests that gonadotropin is an important factor for death of river lampreys, but that in males another hypophysial factor may be involved. Corticosteroids, which may play an important role in the similar death after spawning in Pacific salmon (see discussion by Larsen 1973), have, as mentioned, not been demonstrated in lampreys; so if corticotropin is involved it may exert its effect directly on the tissues of the body.

The effects of hypophysectomy and gonadectomy on survival indicate that gonadotropin might exert part of its deadly effect via sex hormones. Treatment of intact lampreys with testosterone implants had no marked effect on survival, however, and estradiol implants surprisingly prolonged survival, especially in males (up to 4 mo). These results support the notion that death after spawning is not a simple consequence of sexual maturation. It may be suggested that the "programme" responsible for death after spawning is a delicate mechanism which may be spoiled in several ways, e.g. by treatment with unnaturally high doses of sex hormone.

Death after spawning is probably closely correlated with exhaustion of body reserves. In the experimental situation where prolonged survival was obtained, the rate of reduction in length of the body was generally slow, indicating that the processes of mobilization of body tissue were slowed down. Beamish et al. (1979) stress the fact that *P. marinus* after spawning still contain more energy reserves than small juvenile lampreys, which had just begun to feed. This indicates that it may not be a simple lack of energy that causes their death, but a more complicated interplay of deterioration of the body, breakdown of regulatory mechanisms, lack of essential substances, and accumulation of poisonous products. It would be interesting to try to prevent death after spawning by supplying sexually mature lampreys with metabolites and other substances by infusion.

General Discussion

As mentioned above, gonadotropin from the pituitary gland appears to be essential in sexual maturation, but how is sexual maturation initiated? The experimental evidence obtained in river lampreys (Larsen 1978a) leads to the conclusion that a rise in temperature and an increase in day length are not essential signals to sexual maturation. Neither does gonadotropin secretion need a stimulatory influence coming from the central nervous system. This was perhaps not to be expected, since the pro- and meso-adenohypophysis is separated by connective tissue from the central nervous system and receives no portal vessels or innervation (Larsen and Rothwell 1972; Gorbman 1980). Regulatory substances might, however, reach the pro- and meso-adenohypophysis by diffusion through the connective tissue and influence the function of the gland, and there seems to be indirect evidence for some sort of central nervous control of the pro- and meso-adenohypophysis in *Eudontomyzon danfordi* (Molnar and Szabo 1973, 1975) (see also Gorbman 1980). The transplantation experiments suggest that a stimulatory central nervous influence is not essential for initiation and maintenance of sexual maturation; however, it cannot be excluded that an inhibitory influence is removed at the time of sexual maturation.

It is characteristic of lampreys that sensitivity of the gonads to gonadotropin and of the body tissues (responsible for development of secondary sex characters) to sex hormones only develops close to the time of natural sexual maturation. How development of this sensitivity is regulated is unknown. Measurement of secretion rates and blood levels of gonadotropin and sex hormones before and during sexual maturation may help us to understand how sexual maturation is initiated. It would also be important to obtain knowledge about the chemical identity of lamprey gonadotropin(s).

Since no external clues or "clock" located in the central nervous system seem to be responsible for initiation of sexual maturation, it was suggested that a metabolic signal might be responsible for increasing gonadotropin and sex hormone secretion and/or increasing sensitivity towards these hormones (Larsen 1973a, 1978a). Teleologically it is reasonable to expect a mechanism securing sexual maturation before the lamprey dies from lack of food intake — and this could be related to exhaustion of fat reserves, for example, and a subsequent phase of protein catabolism. This is not likely, since fat is utilized together with protein in a parallel time course (see above), so there seems to be no qualitative shift in metabolism at the time when sexual maturation is initiated. There is, however, a quantitative shift, also reflected in increased rate of reduction in length and increased oxygen uptake. We do not know how this shift is accomplished, except that the presence of the pituitary gland is essential for its occurrence. It was mentioned previously that upstream migration, even within one species, may occur nearly one year before spawning or only a month before. This fact was used to exclude the possibility that the start of upstream migration triggers some events which, after a well-defined period of time, initiate sexual maturation (Larsen 1978a). This conclusion may be false; there may be genetic strains of river lampreys each with their well-defined time lag between migration and sexual maturation. There is a deplorable lack of knowledge about possible genetic differences between lampreys migrating early or late and between large and small lampreys. The very small early spring migrants of *L. fluviatilis*, which are supposed to spawn late, mentioned by Potter and Huggins (1973), could well belong to a special genetic strain. My own experience is that the very small and the very large lampreys caught in the same river at the same time in autumn (see p. 1764) become sexually mature at the same time. Furthermore we do not know exactly when lampreys stop feeding; it is perhaps not safe to conclude that the size of the intestine and its ability to support marine osmoregulation reflect the time the lampreys have been without food (see the discussion on p. 1764).

Parasitic lampreys may be induced to stop feeding at a well-defined time, and then sexual maturation may occur at a fixed time after that. Nonparasitic lampreys stop feeding before metamorphosis, and in these the time of metamorphosis might constitute a time when a similar regulated process is started, which had sexual maturation built in as a consequence — but the mechanism behind such a postulated endogenous "hour-glass" model is totally unknown. Metamorphosis by itself seems not to be an essential prerequisite for sexual maturation, since Zanandrea (1956) found some neotenic *L. planeri* larvae, one with fully developed eggs and secondary sex characters, others with visible eggs but no secondary sex characters.

With such a complicated phenomenon as sexual maturation it may be naive to look for *an* external signal or *an* internal factor that initiates it. On the other hand you cannot investigate complex problems without making simple assumptions in the beginning. The only safe conclusion today seems to be that sexual maturation relies on a complex interplay of ill-defined maturation processes in the hypophysis (and brain ?), in the gonads, and in the peripheral tissues. The maturation processes are intimately connected with the processes related to synchony, and gonadotropin and sex hormones play important roles in the normal course of synchony and sexual maturation which lead to death after spawning.

ABOU-SEEDO, F. S., AND I. C. POTTER. 1979. The estuarine phase in the spawning run of the river lamprey *Lampetra fluviatilis*. J. Zool. Lond. 188: 5–25.

ANDERSON, W. C., AND P. J. MANION. 1977. Morphological development of the integument of the sea lamprey, *Petromyzon marinus*. J. Fish. Res. Board Can. 34: 159–163.

APPLEGATE, V. C. 1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. Special Scientific Report: Fisheries 55: 237 p.

APPLEGATE, V. C., AND B. R. SMITH. 1950. Sea lamprey spawning runs in The Great Lakes, 1950. Special Scientific Report: Fisheries 61: 49 p.

APPLEGATE, V. C., AND M. L. H. THOMAS. 1965. Sex ratios and sexual dimorphism among recently transformed sea lampreys, *Petromyzon marinus* Linnaeus. J. Fish. Res. Board Can. 22: 695–711.

BAHR, K. 1952. Beiträge zur Biologie des Flussneunauges *Petromyzon fluviatilis* L. (Lebensraum and Ernährung). Zool. Jahrb. (Syst.) 81: 408–436.

BASSETT, J. R., F. L. STRAND, AND K. D. CAIRNCROSS. 1978. Glucocorticoids, adrenocorticotropic hormone and related polypeptides on myocardial sensitivity to noradrenaline. Europ. J. Pharmacol. 49: 243–249.

BEAMISH, F. W. H. 1979. Migration and spawning energetics of the anadromous sea lamprey, *Petromyzon marinus*. Environ. Biol. Fish. 4: 3–7.

BEAMISH, F. W. H., I. C. POTTER, AND E. THOMAS. 1979. Proximate composition of the adult anadromous sea lamprey, *Petromyzon marinus* L., in relation to feeding, migration and reproduction. J. Anim. Ecol. 48: 1–19.

BENTLEY, P. J., AND B. K. FOLLETT. 1965a. Fat and carbohydrate reserves in the river lamprey during spawning migration. Life Sci. 4: 2003–2007.

1965b. The effects of hormones on the carbohydrate metabolism of the lamprey *Lampetra fluviatilis*. J. Endocrinol. 31: 127–137.

BERG, L. S. 1931. A review of the lampreys of the northern hemisphere. Ann. Mus. Zool. Ed. Akad. Sci. URRS 32: 87–116.

BERINGER, T., AND R. HADEK. 1972. Cardiac innervation in the lamprey (*Petromyzon marinus*). Anat. Rec. 172: 269–270.

BERTOLINI, B. 1965. The structure of the liver cells during the life cycle of a brook-lamprey (*Lampetra zanandreai*). Z. Schr. Zellforsch. 67: 297–318.

BRINN, J. E., AND A. EPPLE. 1976. New types of islet cells in a cyclostome, *Petromyzon marinus* L. Cell Tissue Res. 171: 317–329.

BUSSON-MABILLOT, S. 1967a. Structure ovarienne chez la lamproie adulte (*Lampetra planeri* Bloch). I. La zone pellucide. Morphogénèse et constitution histochimique. J. Microsc. 6: 577–598.

1967b. Structure ovarienne de la lamproie adulte (*Lampetra planeri* Bloch). II. Les enveloppes de l'ovocyte: cellules folliculaires et stroma ovarien. J. Microscopie 6: 807–838.

BUUS, O., AND L. O. LARSEN. 1975. Absence of known corticosteroids in blood of river lampreys (*Lampetra fluviatilis*) after treatment with mammalian corticotropin. Gen. Comp. Endocrinol. 26: 96–99.

CLARIDGE, P. N., AND I. C. POTTER. 1975. Oxygen consumption, ventilatory frequency and heart rate of lampreys (*Lampetra fluviatilis*) during their spawning run. J. Exp. Biol. 63: 193–206.

DE VOS, R., C. DE WOLF-PEETERS, AND V. DESMET. 1973. A morphologic and histochemical study of biliary atresia in lamprey liver. Z. Zellforsch. 136: 85–96.

DOCKRAY, G. J., AND A. D. PICKERING. 1972. The influence of the gonad on the degeneration of the intestine in migrating river lampreys: *Lampetra fluviatilis* L. (Cyclostomata). Comp. Biochem. Physiol. 43A: 279–286.

DODD, J. M. 1965. Endocrine patterns in the reproduction of lower vertebrates. Proc. 2. Int. Congr. Endocrinol. 1: 124–130. Excerpta Med., London.

1972. Ovarian control in cyclostomes and elasmobranchs. Am. Zool. 12: 325–339.

DODD, J. M., AND J. P. WIEBE. 1968. Endocrine influences on spermatogenesis in cold blooded vertebrates. Arch. Anat. Histol. Embryol. 51: 157–174.

EDDY, J. M. P. 1972. The pineal complex, p. 91–103. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. II. Academic Press, London.

EPPLE, A., AND J. E. BRINN. 1975. Islet histophysiology: evolutionary correlations. Gen. Comp. Endocrinol. 27: 320–349.

ESSÉN, B., E. JANSSON, J. HENRIKSSON, A. W. TAYLOR, AND B. SALTIN. 1975. Metabolic characteristics of fibre types in human skeletal muscle. Acta Physiol. Scand. 95: 153–165.

Fontaine, M. 1958. Classe des cyclostomes, p. 13–425. *In* Traité de zoologie, Vol. XII. Masson, Paris.

Fontaine, Y.-A. 1975. Hormones in fishes. Biochem. Biophys. Perspect. Mar. Biol. 2: 139–212.

Frisch, R. E. 1976. Fatness of girls from menarche to age 18 years, with a normogram. Hum. Biol. 48: 353–359.

George, J. C., and F. W. H. Beamish. 1974. Haemocytology of the supraneural myeloid body in the sea lamprey during several phases of life cycle. Can. J. Zool. 52: 1585–1589.

Gorbman, A. 1980. Evolution of the brain–pituitary relationship: evidence from the Agnatha. Can. J. Fish. Aquat. Sci. 37: 1680–1686.

Govyrin, V. A. 1967. The trophic function of sympathetic nerves in the heart and skeletal muscles. Nauka, Leningrad. (A monograph in Russian)

Govyrin, V. A., and D. I. Popova. 1965. Adrenergic innervation of adipose tissue in vertebrates. Zh. Evol. Biokhim. Fiziol. 1: 337–342. (In Russian, English Summary)

Hagelin, L. O. 1959. Further aquarium observations on the spawning habits of the river lamprey (*Petromyzon fluviatilis*). Oikos 9: 221–238.

Hardisty, M. W. 1956. Some aspects of osmotic regulation in lampreys. J. Exp. Biol. 33: 431–447.

1971. Gonadogenesis, sex differentiation and gametogenesis, p. 295–359. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London.

1978. Primordial germ cells and the vertebrate germ line, p. 1–45. *In* R. E. Jones [ed.] The vertebrate ovary, comparative biology and evolution. Plenum Press, New York.

Hardisty, M. W., and I. C. Potter. 1971. The general biology of adult lampreys, p. 127–206. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London.

Hoar, W. S. 1976. Smolt transformation: evolution, behavior and physiology. J. Fish. Res. Board Can. 33: 1233–1252.

Ivanova-Berg, M. M. 1933. Zur Biologie des Flussneunauges (*Lampetra fluviatilis* L.). Arch. Hydrobiol. 25: 22–37.

1936. Spring migration and spawning of the Neva river lamprey. Bull. Acad. Sci. USSR, Ser. Biol. 1: 599–604. (In Russian, English Summary)

John, T. M., E. Thomas, J. C. George, and F. W. H. Beamish. 1977. Effect of vasotocin on plasma free fatty acid level in the migrating anadromous sea lamprey. Arch. Int. Physiol. Biochim. 85: 865–870.

Joss, J. M. P. 1973. Pineal–gonad relationships in the lamprey *Lampetra fluviatilis*. Gen. Comp. Endocrinol. 21: 118–122.

Karlsson, J., B. Diamant, and B. Saltin. 1970. Muscle metabolites during submaximal and maximal exercise in man. Scand. J. Clin. Lab. Invest. 26: 385–394.

Kelényi, G., and L. O. Larsen. 1976. The haematopoietic supraneural organ of adult, sexually immature river lampreys (*Lampetra fluviatilis* (L.) Gray) with particular reference to azurophil leucocytes. Acta Biol. Acad. Sci. Hung. 27: 45–56.

Kennedy, G. C., and J. Mitra. 1963. Body weight and food intake as initiating factors for puberty in the rat. J. Physiol. 166: 408–418.

Kille, R. A. 1960. Fertilization of the lamprey egg. Exp. Cell Res. 20: 12–27.

Knowles, F. G. W. 1939. The influence of anterior-pituitary and testicular hormones on the sexual maturation of lampreys. J. Exp. Biol. 16: 535–547.

Koch, H. J. A. 1968. Migration, p. 305–349. *In* E. J. W. Barrington and C. B. Jørgensen [ed.] Perspectives in endocrinology, hormones in the lives of lower vertebrates. Academic Press, London.

Kott, E. 1970. Differences between the livers of spawning male and female sea lamprey (*Petromyzon marinus*). Can. J. Zool. 48: 745–750.

1973. Epidermal pigmentation in the sea lamprey *Petromyzon marinus* L. Can. J. Zool. 51: 101–104.

Krohn, P. L. 1966. Topics in the biology of aging. Interscience Publ., John Wiley and Sons, New York.

Lanzing, W. J. R. 1959. Studies on the river lamprey, *Lampetra fluviatilis*, during its anadromous migration. Thesis, Uitgeversmaatschappij Neerlandia, Utrecht. 82 p.

Larsen, L. O. 1962. Weight and length in the river lamprey. Nature 194: 1093.

1965. Effects of hypophysectomy in the cyclostome, *Lampetra fluviatilis* (L.) Gray. Gen. Comp. Endocrinol. 5: 16–30.

1970. The lamprey egg at ovulation (*Lampetra fluviatilis* L. Gray). Biol. Reprod. 2: 37–47.

1972. Endocrine control of intestinal atrophy in normal lampreys and of intestinal hypertrophy in gonadectomized lampreys, *Lampetra fluviatilis*. Gen. Comp. Endocrinol. 18: 602 (abstr.).

1973. Development in adult, freshwater river lampreys and its hormonal control. Starvation, sexual maturation and natural death. Thesis, University of Copenhagen, Copenhagen. 172 p.

1974. Effect of testosterone and oestradiol on gonadectomized and intact male and female river lampreys (*Lampetra fluviatilis* (L.) Gray). Gen. Comp. Endocrinol. 24: 305–313.

1976a. Blood glucose levels in intact and hypophysectomized river lampreys (*Lampetra fluviatilis* L.) treated with insulin, 'stress', or glucose, before and during the period of sexual maturation. Gen. Comp. Endocrinol. 29: 1–13.

1976b. Regulation of blood glucose in the river lamprey: the possible physiological role of insulin and hyperglycemic hormones, p. 285–290. *In* T. A. I. Grillo, L. Leibson, and A. Epple [ed.] The evolution of pancreatic islets. Pergamon Press, Oxford.

1978a. Hormonal control of sexual maturation in lampreys, p. 105–108. *In* P. J. Gaillard and H. H. Boer [ed.] Comparative endocrinology. Elsevier/North-Holland Biomedical Press, Amsterdam.

1978b. Subtotal hepatectomy in intact or hypophysectomized river lampreys (*Lampetra fluviatilis* L.): effects on regeneration, blood glucose regulation, and vitellogenesis. Gen. Comp. Endocrinol. 35: 197–204.

Larsen, L. O., and P. Rosenkilde. 1971. Iodine metabolism in normal, hypophysectomized, and thyrotropin treated river lampreys (*Lampetra fluviatilis* (Gray) L. — Cyclostomata). Gen. Comp. Endocrinol. 17: 94–104.

Larsen, L. O., and B. Rothwell. 1972. Adenohypophysis, p. 1–67. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Academic Press, London.

Leibson, L., and E. M. Plisetskaya. 1968. Effect of insulin on blood sugar level and glycogen content in organs of some cyclostomes and fish. Gen. Comp. Endocrinol. 11: 381–392.

Leibson, L., E. Plisetskaya, and B. Leibush. 1976. The comparative study of mechanism of insulin action on muscle carbohydrate metabolism, p. 345–362. *In* T. A. I.

Grillo, L. Leibson, and A. Epple [ed.] The evolution of pancreatic islets. Pergamon Press, Oxford.

Lewis, S. V. 1980. Respiration of lampreys. Can. J. Fish. Aquat. Sci. 37: 1711–1722.

Lowry, O. H., N. J. Rosebrough, A. L. Farr, and R. J. Randall. 1951. Protein measurement with the Folin phenol reagent. J. Biol. Chem. 193: 265–275.

Manion, P. J., and A. L. McLain. 1971. Biology of larval sea lampreys (*Petromyzon marinus*) of the 1960 year class, isolated in the Big Garlic River, Michigan, 1960–65. Great Lakes Fishery Comm. Tech. Rep. 16: 35 p.

Manion, P. J., and G. W. Piavis. 1977. Dentition throughout the life history of the landlocked sea lamprey, *Petromyzon marinus*. Copeia 1977: 762–766.

Manion, P. J., and B. R. Smith. 1978. Biology of larval and metamorphosing sea lampreys, *Petromyzon marinus*, of the 1960 year class in the Big Garlic River, Michigan. Part II 1966–1972. Great Lakes Fish. Comm. Tech. Rep. 30: 35 p.

Marinelli, W., and A. Strenger. 1954. Vergleichende Anatomie und Morphologie der Wirbeltiere. Franz Deuticke, Wien.

Mazeaud, M. 1969. Adrénalinémie et noradrénalinémie chez la lamproie marine (*Petromyzon marinus* L.). C. R. Soc. Biol. 163: 349–352.

Miescher, F. 1880. Statistische und biologische Beiträge zur Kenntniss vom Leben des Rheinlachses im Süsswasser. Zur internationalen Fischereianstellung in Berlin, Leipzig 1880. Reprinted in Die histochemischen und physiologischen Arbeiten von F. Miescher, 1897, Vol. II, p. 116–192.

1890. Biologische Studien über das Leben des Rheinlachses im Süsswasser. Reprinted in Die histochemischen und physiologischen Arbeiten von F. Miescher. p. 304–324.

1892. Physiologische Fragmente über den Rheinlachs. Reprinted in Die histochemischen und physiologischen Arbeiten. p. 325–327.

Minelli, G., and M. C. Rossini. 1961. Struttura e rapporti vascolari del fegato nella larva e nell'adulto di lampreda (*Lampetra planeri*). Arch. Ital. Anat. Embriol. 66: 385–406.

Mislin, H. 1941. Der Phasenwechsel des Rheinlachses (*Salmo salar* L.) unter besonderer Berüchsichtigung des Ernährungsapparates. Rev. Suisse Zool. 48 (Suppl. 1): 1–181.

Molnar, B., and S. Szabó. 1973. Aspects cytologiques des cellules gonadotropes et de la neurosecretion preoptico-neurohypophysaire pendant le cycle ovarien chez *Eudontomyzon danfordi*. Stud. Univ. Babes-Bolyai, Ser. Biol. 18: 105–113. (In Rumanian, French Summary)

1975. Actinunea clorpromazinei asupra sistemului neurosecretor hipotalamo-hipofizar la *Eudontomyzon danfordi* Regan. Stud. Cercet. Biol., Ser. Biol. An. 27: 101–104. (In Rumanian, English Summary.)

Moore, J. W., and I. C. Potter. 1976. Aspects of feeding and lipid deposition and utilization in lampreys, *Lampetra fluviatilis* (L) and *Lampetra planeri* (Bloch). J. Anim. Ecol. 45: 699–712.

Morris, R. 1972. Osmoregulation, p. 193–239. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. II. Academic Press, London.

1980. Blood composition and osmoregulation in ammocoete larvae. Can. J. Fish. Aquat. Sci. 37: 1665–1679.

Murat, J. C., E. M. Plisetskaya, and L. P. Soltitskaya. 1979. Glucose-6-phosphatase activity in kidney of the river lamprey (*Lampetra fluviatilis* L.). Gen. Comp. Endocrinol. 39: 115–117.

Müller, H. 1968. Feinstruktur und Lipidbildung der Fettzellen im Perimeningealgewebe von Neunaugen unter normalen und experimentellen Bedingungen. Z. Schr. Zellforsch. 84: 858–608.

Natochin, Yu. V. 1972. Glomerular filtration and proximal reabsorption rates in evolution of the kidney in vertebrates. J. Evol. Biochem. Physiol. 8: 289–296. (In Russian)

Nicoll, C. S. 1974. Physiological actions of prolactin, p. 253–292. *In* E. Knobil and W. H. Sawyer [ed.] Handbook of physiology, Sect. 7, Endocrinology, Vol. IV, The pituitary gland, part 2. Am. Physiol. Soc., Washington.

Oakley, E. H. N., L. O. Larsen, and B. Saltin. 1980. Changes in lipid, glycogen, protein, and enzyme activities of the river lamprey (*Lampetra fluviatilis* L.) before and during the period of sexual maturation. (In preparation)

O'Boyle, R. N., and F. W. H. Beamish. 1977. Growth and intermediary metabolism of larval and metamorphosing stages of the landlocked sea lamprey, *Petromyzon marinus* L. Environ. Biol. Fish. 2: 103–120.

Phillips, J. W., and F. J. R. Hird. 1977a. Gluconeogenesis in vertebrate livers. Comp. Biochem. Physiol. 57B: 127–131.

1977b. Ketogenesis in vertebrate livers. Comp. Biochem. Physiol. 57B: 133–138.

Piavis, G. W., N. H. Dubin, and B. Nardell. 1975. The 'estradiol fraction' in peripheral blood of the lamprey, *Petromyzon marinus*. Anat. Rec. 181: 449–450.

Pickering, A. D. 1970. Osmoregulation and endocrinology of lampreys. Ph.D. thesis, The University of Nottingham, England.

1972. Effects of hypophysectomy on the activity of the endostyle and thyroid gland in the larval and adult river lamprey, *Lampetra fluviatilis* L. Gen. Comp. Endocrinol. 18: 335–343.

1976a. Stimulation of intestinal degeneration by oestradiol and testosterone implantation in the migrating river lamprey, *Lampetra fluviatilis* L. Gen. Comp. Endocrinol. 30: 340–346.

1976b. Effects of gonadectomy, oestradiol and testosterone on the migrating river lamprey, *Lampetra fluviatilis* (L). Gen. Comp. Endocrinol. 28: 473–480.

1976c. Iodide uptake by the isolated thyroid gland of the river lamprey, *Lampetra fluviatilis* (L). Gen. Comp. Endocrinol. 28: 358–364.

Pickering, A. D., and G. J. Dockray. 1972. The effects of gonadectomy on osmoregulation in the migrating river lamprey: *Lampetra fluviatilis* L. Comp. Biochem. Physiol. 41A: 139–147.

Plisetskaya, E., B. N. Leibush, and V. Bondareva. 1976. The secretion of insulin and its role in cyclostomes and fishes, p. 251–269. *In* T. A. I. Grillo, L. Leibson, and A. Epple [ed.] The evolution of pancreatic islets. Pergamon Press, Oxford.

Plisetskaya, E. M., and T. I. Mazina. 1969. The influence of hormones on nonesterified fatty acids in the blood of the Baltic lamprey *Lampetra fluviatilis*. Zh. Evol. Biokhim. Fiziol. 5: 457–463. (In Russian, English Summary, translation by Plenum Publ. Corp., New York)

Polyakova, T. I., and E. M. Plisetskaya. 1977. Cytological and functional properties of islet tissue in lampreys (*Lampetra fluviatilis*) on different stages of their life cycle. Citologia 19: 1238–1244. (In Russian, English Summary)

Potter, I. C., and F. W. H. Beamish. 1977. The freshwater biology of adult anadromous sea lampreys *Petromyzon marinus*. J. Zool. 181: 113–130.

1978. Changes in haematocrit and haemoglobin concentration during the life cycle of the anadromous sea lamprey, *Petromyzon marinus* L. Comp. Biochem. Physiol. 60A: 431–434.

Potter, I. C., and R. J. Huggins. 1973. Observations on the morphology, behaviour and salinity tolerance of downstream migrating river lampreys (*Lampetra fluviatilis*). J. Zool. Lond. 169: 365–379.

Potter, I. C., R. Perry, and J. H. Youson. 1978. A proposal for the adaptive significance of the development of the lamprey fat column. Acta Zool. (Stockh.) 59: 63–67.

Read, L. J. 1968. A study of ammonia and urea production and excretion in the fresh-water-adapted form of the Pacific lamprey, *Entosphenus tridentatus*. Comp. Biochem. Physiol. 26: 455–466.

Rovainen, C. M. 1980. Neurophysiology of lampreys. Can. J. Fish. Aquat. Sci. 37: 1723–1738.

Rovainen, C. M., G. E. Lemcoe, and A. Peterson. 1971. Structure and chemistry of glucose-producing cells in meningeal tissue of the lamprey. Brain Res. 30: 99–118.

Savina, M. V., and E. M. Plisetskaya. 1976. Synthesis of glycogen from glycerol in isolated tissues of the lamprey *Lampetra fluviatilis*. Zh. Evol. Biokhim. Fiziol. 12: 282–284. (In Russian)

Savina, M. V., and A. B. Wojtczak. 1977. Enzymes of gluconeogenesis and the synthesis of glycogen from glycerol in various organs of the lamprey (*Lampetra fluviatilis*). Comp. Biochem. Physiol. 57B: 185–190.

Schreibman, M. P., and K. D. Kallman. 1978. The genetic control of sexual maturation in the teleost, *Xiphophorus maculatus* (Poeciliidae); a review. Ann. Biol. Anim. Biochem. Biophys. 18: 957–962.

Sjöberg, K. 1977. Locomotor activity of river lamprey *Lampetra fluviatilis* (L.) during the spawning season. Hydrobiologia 55: 265–270.

Smitten, N. A. 1972. Sympatho-adrenal system in phylo- and ontogenesis of the vertebrates. Nauka, Moscow. (A monograph in Russian)

Stabrowsky, E. M. 1967. The distribution of adrenalin and noradrenalin in the organs of the Baltic lamprey (*Lampetra fluviatilis*) at rest and under various functional stresses. Zh. Evol. Biokhim. Fiziol. 3: 216–221. (In Russian, English Summary).

Sterba, G. 1952. Die Neunaugen. Akad. Verlagsges., Geest and Portig, Leipzig.

Tesch, W.-F. 1967. Aktivität und Verhalten wandernder *Lampetra fluviatilis*, *Lota lota* und *Anguilla* im Tidegebiet der Elbe. Helgol. Wiss. Meeresunters. 16: 92–111.

Tilik, Z. E. 1932. Chemical composition of the Neva lamprey. Bull. Inst. Freshwater Fish. Leningr. 14: 149–153. (In Russian)

Tuunainen, P., E. Ikonen, and H. Auvinen. 1980. Lampreys and lamprey fisheries in Finland. Can. J. Fish. Aquat. Sci. 37: 1953–1959.

Vladykov, V. D., and G. N. Mukerji. 1961. Order of succession of different types of infraoral lamina in landlocked sea lamprey (*Petromyzon marinus*). J. Fish. Res. Board Can. 18: 1125–1143.

Weisbart, M., J. H. Youson, and J. P. Wiebe. 1978. Biochemical, histochemical, and ultrastructural analyses of presumed steroid-producing tissues in the sexually mature sea lamprey, *Petromyzon marinus* L. Gen. Comp. Endocrinol. 34: 26–37.

Weissenberg, R. 1927. Beiträge zur Kenntnis der Biologie und Morphologie der Neunaugen. II. Das Reifewachstum der Gonaden bei *Lampetra fluviatilis* und *planeri*. Z. Schr. Mikrosk.-Anat. Forsch. 8: 193–249.

Yamamoto, T. 1944. On the excitation–conduction gradient in the unfertilized egg of the lamprey, *Lampetra planeri*. Proc. Imp. Acad. Tokyo 20: 30–35.

Yorke, M. A., and D. B. McMillan. 1979. Nature and cellular origin of the adhesive coats of the lamprey egg (*Petromyzon marinus*). J. Morphol. 162: 313–326.

Zanandrea, G. 1956. Neotenia in *Lampetra planeri zanandreai* (Vladykov) e l'endocrinologia sperimentale dei ciclostomi. Boll. Zool. 23: 412–427.

1957. Esame critico e comparativo delle lamprede catturate in Italia. Arch. Zool. Ital. 42: 249–307.

1959. *Lampetra fluviatilis* catturata in mare nel Golfo di Gaeta. Pubbl. Staz. Zool. Napoli 31: 265–307.

Sea Lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: History of Invasion and Control, 1936–78[1]

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Sea lamprey (*Petromyzon marinus*) entered the upper three Great Lakes in the late 1930s and began making sharp inroads into the fish stocks by the mid-1940s in lakes Huron and Michigan and the mid-1950s in Lake Superior. The first serious attempts to control the parasite began in 1950 with the installation of mechanical barriers along the United States shore of Lake Huron to block spawning runs. Electrical barriers, developed in 1952, were installed in 132 tributaries of the Great Lakes by 1960, but control measures did not become effective until after 1958, when a selective toxicant — the lampricide 3-trifluoromethyl-4-nitrophenol (TFM) — was used to destroy larval lampreys in streams. In the 21 years, 1958–78, 1223 treatments of tributaries of the upper three lakes with TFM were completed in 334 streams — 91 in Canada and 243 in the United States. Evidence of the success of the control program was soon obvious: first by reduced sea lamprey spawning runs as measured by the numbers of adults taken at electrical barriers; second by significant decreases in the incidence of sea lamprey wounds on lake trout (*Salvelinus namaycush*); and finally by the excellent responses of major fish stocks to sea lamprey control. All three of the upper lakes have large numbers of lake trout, coho salmon (*Oncorhynchus kisutch*), chinook salmon (*O. tshawytscha*), and other salmonids available to the sport fishery and in some areas to the commercial fishing industry. Although the sea lamprey control program has been successful, it is important that emphasis be placed on developing new and innovative methods to reduce the dependence on lampricides. It is expected that a fully integrated program will eventually comprise several methods, including permanent barrier dams on selected streams and the use of sterilants, attractants, repellents, and biological controls, as well as chemical lampricides.

Key words: sea lamprey, distribution, abundance, history, predation, integrated controls, Huron, Michigan, Superior

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La grande lamproie marine (*Petromyzon marinus*) pénétra dans les trois Grands Lacs supérieurs à la fin des années 1930, et ses effets sur les stocks de poissons commencèrent à se faire sentir sérieusement dès le milieu des années 1940 dans les lacs Huron et Michigan et le milieu des années 1950 dans le lac Supérieur. Les efforts en vue de contrôler le parasite commencèrent en 1950, alors qu'on installait des barrières mécaniques le long de la rive américaine du lac Huron dans le but de bloquer les remontées de ponte. Il y avait en 1960 des barrières électriques mises au point en 1952 dans 132 tributaires des Grands Lacs, mais ce n'est qu'après 1958 que les mesures de contrôle devinrent effectives, avec l'introduction d'un toxique sélectif — le lampricide 3-trifluorométhyl-4-nitrophénol (TFM) — pour détruire les lamproies larvaires dans les cours d'eau. Pendant ces 21 ans, soit de 1958 à 1978, on a effectué 1223 traitements au TFM dans 334 cours d'eau tributaires des trois lacs supérieurs — 91 au Canada et 243 aux États-Unis. On se rendit rapidement compte du succès du programme de contrôle: d'abord par la diminution des remontées de ponte des lamproies, tel qu'indiqué par le nombre des adultes capturés aux barrières électriques; ensuite par une diminution marquée d'occurrence de cicatrices de lamproies sur le touladi (*Salvelinus namaycush*); et enfin par l'excellente réponse des principaux stocks de poissons au contrôle de la lamproie. Les trois Grands Lacs

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supérieurs contiennent tous un grand nombre de touladis, saumons coho (*Oncorhynchus kisutch*), saumons chinook (*O. tshawytscha*) et autres salmonidés accessibles à la pêche sportive et, dans certaines régions, à une pêche commerciale. Malgré le succès du programme de contrôle de la grande lamproie marine, il est important de mettre l'accent sur la mise au point de méthodes nouvelles et innovatrices afin de réduire la dépendance des lampricides. On s'attend qu'un programme pleinement intégré comprendra éventuellement plusieurs méthodes, y compris barrages permanents dans des cours d'eau choisis et utilisation de substances stérilisantes, attirantes ou repoussantes, contrôles biologiques, aussi bien que lampricides chimiques.

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THE five Great Lakes of the United States and Canada form the largest group of freshwater lakes in the world; and Lake Superior, the most northerly and westerly of the group, is the world's largest in area. The total area of the five lakes is about 25 million ha, or more than 245 000 km^2 — about 157 000 km^2 in the United States and 88 000 km^2 in Canada (Smith 1971); total shoreline length is about 15 000 km, and the natural drainage basin covers nearly 746 000 km^2.

Lake Superior lies almost entirely within the Canadian Shield, an area of old (pre-Cambrian) rocks, and the other four — lakes Michigan, Huron, Erie, and Ontario — lie mostly in a younger (Paleozoic) rock formation, consisting mainly of limestones, dolomites, shales, and sandstones.

The eight states of the United States that border the Great Lakes contain about 39% of the total U.S. population. The Province of Ontario, bordering four of the lakes, is the most populous of the Canadian provinces. In all, more than 60 million people live, work, and play in the Great Lakes area.

The fur trade paved the way for the exploration and eventual settlement of the Great Lakes region. The lakes themselves were the original avenues of transportation, and now serve to carry millions of tons of iron ore, grain, coal, and other products each year. Even before the arrival of the Europeans, Indians were harvesting the abundant fish from the Great Lakes, and commercial fishing was one of the first industries developed in the area.

About 125 species of fish, mostly confined to shoals and bays, inhabited the Great Lakes. Interspecific competition, especially in the open water areas, was relatively low before invasion by the sea lamprey (*Petromyzon marinus*). Only two predators — lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*) — were present in the deep waters of the larger lakes; they fed on some 15 species of forage fish, which in turn fed on plankton and bottom fauna (Smith 1968).

A series of biological changes took place when the sea lamprey moved into the three upper Great Lakes (Superior, Michigan, and Huron). These changes have had far-reaching effects extending beyond the lake trout and other species that were directly attacked by the parasite. The seriousness of the threat posed by sea lamprey was not generally recognized until the invader was well established in all the lakes and had seriously affected the fisheries of Lakes Michigan and Huron. As the sea lamprey increased, primarily at the expense of the stocks of lake trout and to a lesser degree of those of other species, the need for research and concerted action was recognized by the commercial fishing industry and fishery investigators of the United States and Canada.

Smith et al. (1974) summarized early efforts to coordinate investigations of the sea lamprey's distribution, life history, and destructiveness by various United States and Canadian agencies; one of the first was the formation of the Great Lakes Sea Lamprey Committee in 1946. This Committee and the Great Lakes Lake Trout Committee were combined in 1952 to form the Great Lakes Lake Trout and Sea Lamprey Committee, which was renamed in 1953 and functioned as the Great Lakes Fishery Committee during 1953–57. Delegates from the U.S. Fish and Wildlife Service, the Fisheries Research Board of Canada, the Ontario Department of Lands and Forests, and each state bordering on the Great Lakes served on these successive committees. In 1953 the Great Lakes Federal–Provincial Fisheries Research Committee, consisting of representatives from the Fisheries Research Board of Canada and the Ontario Department of Lands and Forests, was formed to investigate the sea lamprey problem in Canadian waters of the Great Lakes.

The need for cooperation between the United States and Canada to resolve problems confronting the fisheries of the Great Lakes had been recognized for many years, and several attempts were made to negotiate a fishery treaty. Interest in development of an acceptable treaty was renewed by the invasion of the upper Great Lakes by the sea lamprey. Representatives of the United States of America and Canada signed a new Convention on Great Lakes Fisheries on September 10, 1954, which became effective when instruments of ratification were exchanged on October 11, 1955 (Crowe 1975).

In 1956 the Great Lakes Fishery Commission began its official functions of developing and implementing measures to control sea lamprey, developing and coordinating fishery research programs, and advising governments on measures to improve the fisheries. The Commission's agents responsible for sea lamprey control and research were the U.S. Fish and Wildlife Service, with field headquarters at Marquette, Michigan, and the Fisheries Research Board of Canada, with field headquarters at London, Ontario. In 1966 the Canadian responsibility for sea lamprey control was transferred from the Fisheries Research Board to the Department of Fisheries with field headquarters at Sault Ste. Marie, Ontario, which became the Department of Fisheries and Forestry, in 1971; the Department of the Environment, Fisheries and Marine Science, in 1976; the Department of Fisheries and the Environment, Fisheries and Marine Service, in 1978; and is now in the Department of Fisheries and Oceans.

The development, problems, and progress of sea lamprey control in the Great Lakes through 1969 were briefly discussed by Smith (1971) and a detailed description of the work on Lake Superior from 1953 to 1970 was given by Smith et al. (1974).

In the present report, we summarize sea lamprey control in the three upper Great Lakes. The migration of sea lampreys from Lake Ontario through the Welland Canal into and through Lake Erie and their eventual dispersal and establishment in Lakes Huron, Michigan, and Superior were major factors in the disruption of the entire fish species composition of those lakes.

Sea Lamprey Invasion of Lakes Huron, Michigan, and Superior

SEA LAMPREY MOVEMENT INTO THE LAKES

The first confirmed sea lamprey from the upper Great Lakes, a 40.5-cm-long specimen attached to a lake trout, was taken from Lake Michigan near Milwaukee, Wisconsin, on March 22, 1936. Later on June 13, a 39.5-cm-long male, presumably on a spawning run, was captured in a tributary of Lake Michigan, Elk Lake Outlet, Antrim County, Michigan. However, the recovery of two immature adults, one less than 23 cm long from Door County, Wisconsin, and the other, 43 cm long from Beaver Island, Michigan, in August and October 1936 (Hubbs and Pope 1937), suggests that spawning runs were established at least 4 yr earlier in Lake Michigan.

No sea lampreys were reported from Lake Huron until 1937, when a spawning run was noted in the Ocqueoc River, Presque Isle County, Michigan (Applegate 1950). It seems reasonable to assume that sea lampreys were present but not observed or reported for several years before 1937.

It has been widely assumed that the rapids and navigational locks and other structures across the St. Marys River at Sault Ste. Marie impeded the movement of sea lampreys into Lake Superior because the first confirmed record reported by Applegate (1950) was an immature adult, 24.1 cm long, taken off Isle Royale in August 1946. Recently, however, we observed in a newspaper clipping from the Marquette (Michigan) Mining Journal, dated May 20, 1938, that Dr John Lowe of the biology department of Northern Michigan College had obtained a live sea lamprey that had been attached to a lake trout, from the Anderson Fish Company of Marquette. The relatively small size of the specimen from Isle Royale reported by Applegate and the distance from Lake Huron (about 400 km) suggest that it may have been produced in a tributary of Lake Superior. Thus it appears that the rapids and locks in the St. Marys River did not appreciably delay migration into Lake Superior.

The rate of establishment of the sea lamprey in the upper Great Lakes depended partly on the suitability of the tributary streams for the species. Three physical factors in streams are essential for successful sea lamprey spawning (Applegate 1950): first, for nest building a suitable substrate of gravel is required that includes at least a small amount of sand or other fine material to which the eggs can adhere, thereby increasing the probability of their retention in the nest; second, current must be flowing unidirectionally over the nest; and third, water temperatures must be suitable. These criteria and the presence of physical barriers were used to evaluate the potential of streams for lamprey production.

An extensive survey of the State of Michigan waters of the upper Great Lakes in 1947 and 1948 indicated that sea lampreys were spawning in 106 streams within the State's boundaries — 34 tributaries of Lake Huron, 68 of Lake Michigan, and 4 of Lake Superior (Applegate 1950). The sea lamprey was thus firmly established in all the Great Lakes, and was already causing prodigious damage to the fish stocks of Lakes Huron and Michigan.

EFFECT OF THE SEA LAMPREY INVASION ON FISH STOCKS

Lakes Huron, Michigan, and Superior had traditionally been the source of large, high-quality, coldwater fish for the markets of the midwest and eastern United States. Lake trout alone supported a long-term average annual commercial catch of 7000 t (1 t = 1000 kg) valued at over $5.5 million in the 1940s.

Lake trout production from Lake Huron dropped from more than 2268 t in 1938 to 76 t in 1954, and continued to decline until the fishery collapsed in 1959. Similarly, in Lake Michigan, the lake trout catch decreased from 2948 t in 1944 to a mere 181 kg in 1953. Production of lake trout remained high in Lake Superior through 1950 (2041 t): however, the effect of lamprey predation (combined with high fishing intensity) drastically reduced the catch to 227 t in 1960 (Baldwin and Saalfeld 1962). The Great Lakes States and Province of Ontario imposed a general closed season on lake trout in 1962 (still in effect in 1978) and permitted commercial fishing only under special permit for biological assessment studies. Ontario permitted, in addition, a quota-managed commercial fishery for lake trout in Lake Superior.

Almost all of the other large fish species in the upper Great Lakes were affected by lamprey predation. Simultaneous with the decline of lake trout was the decimation of the burbot. The burbot is not a valuable commercial species; the average yearly catch was only 20 t from Lake Michigan in 1936–45. High sea lamprey scarring rates on lake whitefish (*Coregonus clupeaformis*), catostomids (*Catostomus* spp. and *Moxostoma* spp.), walleye (*Stizostedion vitreum vitreum*), and rainbow trout (*Salmo gairdneri*) were reported frequently, and the fisheries for these species were also drastically reduced.

The ecological balance among species that existed in the three lakes was adversely affected, and the indirect effect of sea lamprey abundance on the succession of smaller species was highly disruptive (Smith 1968). In Lake Michigan there were, before 1945, seven species of ciscoes (*Coregonus* spp.) — commonly called chubs in the commercial fishery — in a relatively static state of abundance. The depletion of lake trout and burbot, the two large predators, favored the survival and increase of their primary food, the ciscoes; the average annual commercial production of ciscoes increased from 2690 t in 1948 to more than 4800 t in 1951–57. After the lake trout and burbot were largely gone, the lamprey was forced to turn to the larger cisco species, and by 1960–61 the two largest species, *Coregonus johannae* and *C. nigripinnis*, were reduced to extinction, or nearly so, and four other species were seriously depleted (Smith 1964). The bloater, *C. hoyi*, the smallest of the cisco species, became very abundant as the predators disappeared.

The changes in Lake Huron apparently were closely similar to those in Lake Michigan.

In the late 1940s another invader from the Atlantic Ocean, alewife (*Alosa pseudoharengus*), entered Lakes Huron and Michigan, and flourished because of the absence of large predators. In Lake Superior, alewife never became abundant, probably because the colder waters of this large, deep lake, near its northern range, are unsuitable for it. The alewife soon affected the species composition of Lakes Michigan and Huron: the abundance of many species, including the bloater, lake herring (*Coregonus artedii*), yellow perch (*Perca flavescens*), and emerald shiner (*Notropis atherenoides*), was greatly reduced.

Abundance and Distribution of Sea Lampreys

GENERAL DISTRIBUTION

The first sea lampreys discovered in the upper Great Lakes were considered scientific curiosities. But by the mid-1940s it became obvious that these predators had destroyed the lake trout in Lake Huron and were rapidly making deep inroads into the lake trout population of Lake Michigan. As a direct result, the first intensive study of the sea lamprey's life history was initiated by the State of Michigan in the Ocqueoc River, a tributary of Lake Huron. Concurrently, in 1946–48, surveys were conducted by conservation officers, questionnaires were circulated to commercial fishermen, a poster campaign was developed to enlist the cooperation of the public, and other sources of information, including organized groups, were consulted (Applegate 1950).

The State of Wisconsin and the Province of Ontario also had intensive studies under way to determine the distribution of the sea lamprey and the impact of its invasion into their waters. Before 1955 almost all observations were of adult lampreys or spawning nests.

The development of a chemical method for the control of sea lamprey larvae in streams (Applegate et al. 1958) prompted various government agencies to perform widespread surveys to determine the presence and distribution of ammocoetes. Most stream surveys were carried out with electroshockers, consisting of a source of electricity and a set of electrodes that conduct pulses of electricity (switch controlled) into the water and the stream bottom. As the electrodes are passed slowly over the stream bottom, the electrically stimulated larvae emerge from their burrows. The lampreys were collected with dip nets and preserved in 5% formalin for later identification (five species of lampreys are found in Great Lakes tributaries) and determination of other biological data. Portable, 110-V, gasoline-powered generators were used initially, but by the mid-1950s more easily portable backpack units were developed consisting of power converters powered by a 6- or 12-V motorcycle battery. In these units, the converters supplied 110-V alternating current to the electrodes (Tibbles 1959; Braem and Ebel 1961). In the late 1960s, efficiency was increased further by the development of a smaller and lighter transistorized model of the backpack shocker that produced pulsed direct current.

The development in 1966 of a formulation of a molluscicide, the 2-aminoethanol salt of 2′,5-dichloro-4′-nitrosalicylanilide (Bayer 73), as a 5% active ingredient on silica sand, provided a useful means for surveying streams where the effectiveness of electroshockers was limited by low conductivity or by deep water over larval habitat. The coated granules, when spread over the water, sink to the stream bottom and cause ammocoetes in the substrate to emerge from their burrows (usually within about 15 min) and come to the surface, where they can be readily collected (Smith et al. 1974).

The movement, abundance, and distribution of sea lampreys in the three upper lakes are discussed in the order in which the principal invasion occurred — Lake Huron, Lake Michigan, and Lake Superior.

LAKE HURON

The original surveys by the State of Michigan indicated that in the Lake Huron watershed of that State, 34 streams were infested with sea lampreys by late 1948. In the Clinton River, tributary to Lake St. Clair, and the Huron River, tributary to Lake Erie near the outlet of the Detroit River, sea lampreys were observed in 1932 and 1938, respectively, but none were found in the later surveys. Sea lampreys were also reported

Table 1. Annual catches of sea lampreys in barriers operated in tributaries of Lake Huron, 1947–78. (Numbers in parentheses show location of streams in Fig. 1.)

		Canada								
			Georgian Bay				Main Basin			
Year	United States, Ocqueoc[a] (33)	North Channel, Kaskawong (93)	Still (71)	Naiscoot (69)	Harris[b] (69)	Mad[c] (62)	Manitou (77)	Blue Jay (76)	Bayfield (52)	Canada total
1965	1390	—	344	38	555	—	—	—	—	937
1966	3273	—	1820	64	904	324	—	—	443	3 555
1967	674	83	1839	103	1532	333	637	957	789	6 273
1968	3418	239	6154	282	1054	413	597	1807	191	10 737
1969	3288	478	1621	68	717	42	144	1130	582	4 782
1970	736	482	558	0	173	8	3	236	128	1 588
1971	2997	271	960	1	445	15	12	332	7	2 043
1972	2847	207	426	2	472	1	11	380	7	1 506
1973	641	135	14	0	8	0	14	22	4	197
1974	911	146	10	0	1	1	4	61	2	225
1975	1901	168	28	0	8	0	8	127	4	343
1976	6937	187	48	0	13	—	—	213	—	461
1977	503	184	1	0	31	—	—	804	—	1 020
1978	2121	209	0	0	13	—	—	—	—	222

[a] Catches in the Ocqueoc River in 1947–64 (except 1956 and 1958) before barriers were installed in Canadian streams were as follows (estimates in 1947 and 1948 based on nest counts): 1947, 10 000; 1948, 13 000; 1949, 24 643; 1950, 18 822; 1951, 19 393; 1952, 9437; 1953, 11 676; 1954, 10 183; 1955, 13 683; 1957, 8163; 1959, 2766; 1960, 7560; 1961, 4715; 1962, 5205; 1963, 4674; 1964, 2677.

[b] Tributary of the Naiscoot River.

[c] Tributary of the Nottawasaga River.

from a number of Canadian rivers in the 1940s, but were not found there in more recent surveys starting in 1956.

In 1944 and 1945, State of Michigan biologists installed a weir and trap in the Ocqueoc River to begin the study of the biology of the sea lamprey. The structure was inefficient and permitted escapement of large numbers of the spawning sea lampreys each year; nevertheless, 3366 sea lampreys were captured and destroyed in 1944 and 4608 in 1945. A permanent mechanical weir and trap were installed in the Ocqueoc River in 1949, and with modifications (converted to an electromechanical weir in 1952) were operated each year in 1949–78 except 1956 and 1958. Except for unaccountable fluctuations in numbers in the later years of the period, the catches from the Ocqueoc River (Table 1) demonstrated generally the changes in sea lamprey abundance in Lake Huron from 1949 to 1978. No weir or trap was operated in 1947 and 1948, but estimates from lamprey nest counts place the spawning runs at about 10 000 and 13 000, respectively. Peak abundance apparently was reached in 1949, when the catch was 24 643 sea lampreys. The numbers remained high (about 19 000) in 1950 and 1951, but for the 4 yr, 1952–55, the catch averaged slightly more than 11 000. Only 2766 sea lampreys were captured in 1959 and by 1965 the catch had dropped to 1390 — less than 6% of the 1949 high. The numbers of spawning-run sea lampreys entering the Ocqueoc River in 1965–78 fluctuated without trend. The largest spawning run for the 14-yr period was 6937 in 1976, followed in 1977 by the all-time low of 503.

The Province of Ontario after querying licensed commercial fishermen about sea lamprey activity before 1946, concluded that the North Channel of Lake Huron was the area being most severely affected by lamprey predation. It was therefore logical for first studies to be in the streams of this area. Several types of traps installed in streams tributary to the North Channel from 1946 to 1949 yielded a total catch of 11 418 adult lampreys in 1946, 6245 in 1947, 6990 in 1948, and 7459 in 1949 (MacKay 1951). The numbers taken each year are not directly comparable because the trapping devices were in different streams each year; however, they do indicate that heavy concentrations of sea lampreys were present in the area at that time.

The Great Lakes Fishery Commission in 1964 approved the installation of several electrical barriers on Canadian tributaries to the North Channel, Georgian Bay, and Lake Huron proper — three relatively independent bodies of water. A total of 12 weirs were installed on 11 tributaries along the Canadian side of the lake, but 2 were operated for only 2 yr, and 2 that were operated for 4 yr did not contribute significantly to the index of sea lamprey abundance. The eight devices that were operated continuously from 1967 to 1975 indicated that sea lamprey spawning runs increased to a peak of 10 737 in 1968 (Table 1). The catch dropped sharply to 4782 in 1969, 1588 in 1970, and 197 in 1973. The catch remained low in 1974 and 1975; three barriers that had taken a combined total of only 18 lampreys per year for 5 yr were removed in 1976.

The systematic inventory of Lake Huron streams for sea lamprey use, as indicated by the presence or absence of ammocoetes, was started in Canada in 1956. Surveys with electric shockers indicated that 24 streams tributary to the North Channel, 7 to Georgian Bay, and 2 to Lake Huron proper (total 33) contained sea lamprey larvae (Great Lakes Fishery Commission 1958). Continuing surveillance disclosed other streams being used by sea lampreys; by 1978, 49 streams tributary to the Canadian shore of Lake Huron contained, or had contained, sea lamprey ammocoete populations.

Distributional surveys for larval sea lampreys were not begun on the U.S. side of Lake Huron until 1961, when 82 streams tributary to the St. Marys River and the north shore of the lake from Detour to St. Ignace were examined. Of these, 17 contained sea lamprey ammocoetes. The first surveys of all U.S. tributaries of Lake Huron (including Lake St. Clair) were completed in 1963; sea lampreys were found in 48 of the 351 streams (Morman 1979). This number had increased to 53 by 1978, bringing to 102 the total number of streams tributary to Lake Huron, in both countries, that contained, or had contained, sea lamprey ammocoetes.

Some ammocoetes migrate downstream into the bays, estuaries, and areas of the lakes at or near the mouths of streams. Sea lamprey larvae in these lake areas are relatively inaccessible, and therefore present a difficult control problem.

Of 53 streams along the U.S. shore that contained sea lamprey ammocoetes, 31 were examined for lake-dwelling populations. (The other 22, for various reasons, did not have the potential to develop such populations.) Twelve areas surveyed contained one or more sea lampreys and nine appeared to harbor significant numbers of ammocoetes. Along the Canadian shore of Lake Huron, biologists found sea lampreys off the mouths of 17 of 18 streams examined by using Bayer 73.

LAKE MICHIGAN

The inventory of sea lamprey spawning streams completed by the State of Michigan in 1947 and 1948 demonstrated the presence of spawning runs in every major watershed in the Lake Michigan basin, involving some 68 streams (Applegate 1950). Wisconsin reported sea lamprey activity in eight rivers, including the Menominee, at the Wisconsin–Michigan border (Great Lakes Sea Lamprey Committee, 1949 mimeograph). In addition, three streams in Indiana were known to support sea lamprey spawning runs (Great Lakes Sea Lamprey Committee, 1949, mimeograph). Sea lamprey spawning was thus confirmed in 79 streams tributary to Lake Michigan by the end of 1949.

Developing interest in selective toxicants for sea lamprey control prompted the initiation in 1955 of surveys for the presence and distribution of sea lamprey ammocoetes in tributaries of northern Lake Michigan (between St. Ignace and Menominee). From 1955 to 1959, sea lamprey larvae were found in 20 of 27 streams examined (Stauffer 1961). The Fish and Wildlife Service and State of Michigan began similar surveys in 1959 and a summary of activities by the end of 1960 indicated that a total of 77 streams were infested by sea lamprey larvae. This number had increased to 99 by 1963 and to 112 by 1978.

Surveys off the mouths of 48 Lake Michigan tributaries that appeared to have the potential for harboring sea lamprey ammocoetes yielded one or more larvae in 20 of the areas, but only 12 appeared to support significant numbers.

LAKE SUPERIOR

Reports of sea lamprey spawning accumulated by the State of Michigan in 1947 and 1948 indicated that only four streams tributary to Lake Superior supported spawning runs of sea lampreys. In 1949, however, sea lampreys were reported taken by commercial fishermen from waters as far west as Minnesota; several were taken off Marquette and Munising, Michigan; and one was collected during lake trout spawn-taking operations at the Montreal River, 129 km north of Sault Ste. Marie, Ontario.

Surveys were conducted from 1950 to 1954 along U.S. and Canadian shores of Lake Superior to determine the number of streams apparently suitable for sea lamprey use. Of 1915 streams inspected (1293 in the United States and 622 in Canada), only 424 (267 in the United States and 157 in Canada) met the physical requirements necessary for sea lamprey production (Loeb and Hall 1952; Loeb 1953; A. H. Lawrie, Great Lakes Research Committee, Appendix 7, 1954, mimeograph) and were thus considered to be potential lamprey producing streams.

The first systematic surveys of streams for presence and distribution of sea lamprey ammocoetes was initiated by the Michigan Department of Natural Resources in 1957 (Stauffer and Hansen 1958). Of 60 river systems surveyed with direct current electric shockers, 21 contained sea lamprey larvae. Later surveys by the U.S. Fish and Wildlife Service increased the number of streams containing sea lampreys to 87 along the U.S. shore.

First surveys of Lake Superior tributaries in Ontario by the Fisheries Research Board of Canada and the Ontario Department of Lands and Forests were largely in inaccessible areas and produced only limited information on ammocoete distribution. Later, more detailed examinations by improved techniques revealed that 60 Canadian tributaries were being used by sea lampreys. By 1978 the total number of Lake Superior tributaries that contained, or had contained, sea lamprey larvae was 147.

Of 47 areas at and off the mouths of the 147 known sea lamprey streams in Lake Superior surveyed, 26 yielded one or more sea lamprey larvae; however, only 19 (9 in the United States and 10 in Canada) appeared to harbor significant populations. In one other area, the St. Marys River above the Sault Ste. Marie Locks, four sea lamprey ammocoetes were captured in an area of over 10 000 m^2 surveyed. Although the numbers caught were small and density was low, the area could become a problem for lamprey control because it is so large (>250 ha).

Sea Lamprey Control — History and Control Techniques

DEVELOPMENT OF CONTROL METHODS

In 1950 a study of sea lamprey life history was completed (Applegate 1950), and the U.S. Fish and Wildlife Service established a field station at Hammond Bay in northern Lake Huron to develop control measures. The life history study indicated that the most vulnerable period in the sea lamprey's life cycle occurs in the stream.

The sea lamprey spawning migration occurs in the spring and early summer during a relatively short time (4–5 mo). Under ideal conditions the adult sea lampreys can be stopped by barriers, either mechanical or electrical, that are installed below suitable spawning areas in the stream. The major disadvantage of this procedure is that the reduction in parasitic stocks will be delayed for many years because several year-classes of larvae already present in the stream must pass through the parasitic phase before the life cycle is interrupted. Also, spawning-phase adults may be diverted into streams that lack barriers.

The destruction of newly metamorphosed sea lampreys during their downstream migration would prevent the parasitism on fish stocks and effect faster control of the lamprey population; however, the migration takes place over a 6-mo or longer period that encompasses the spring and fall seasons, when the largest volumes of water must be screened. The direction of flow and speed of the current favors the downstream passage of the young lampreys past a screen or through an electrical field, and because the animals are small and would be exposed to electricity for only a short time, power requirements to provide a lethal shock would be prohibitive.

In the larval stage all generations of the lamprey are in the streams and vulnerable to attack. The population is relatively sedentary, and the effects of control are immediate. The major disadvantage is that the ammocoetes are usually dispersed over large areas in the streams and sometimes off their mouths.

The need for immediate control imposed by the enormous destruction of lake trout and other fish by the sea lamprey prompted the installation in 1950 and 1951 of 21 mechanical or screen-type weirs and one electric screen to block upstream migration in Canadian and United States tributaries to the three upper lakes; 12 were located in streams of northern Lake Huron, 7 along the west and south shores of Lake Michigan, and 2 along the south shore of Lake Superior (Applegate and Smith 1951; Applegate et al. 1952). These structures immediately provided partial control and a method from which information on costs and problems of larger programs could be developed, and demonstrated the value of limited sea lamprey control on local fish stocks. In addition, they provided localities for developing and testing improvements in such devices, and an opportunity for comparing the effectiveness of new equipment and methods.

Concurrently, research was progressing on several alternate methods of control. The most promising ones were improvements in barrier devices through the use of electricity and the development of chemical lampricides.

Mechanical devices proved to be expensive to build and operate and were difficult to maintain in most streams during the periods of ice-breakup and floods; frequent breakdowns permitted sea lampreys to pass upstream and spawn.

A simple, alternating current electrical field substituting for the screens or grates of a mechanical weir proved to be effective for controlling all upstream movement of lampreys and other fishes, while permitting free downstream passage of flood waters, ice, and debris. Preliminary tests in 1952 demonstrated that an effective and practical electromechanical (electrical barrier and mechanical trap) sea lamprey weir could be built and operated at considerably less cost and with greater efficiency than a purely mechanical device.

By 1960, 162 electromechanical barriers had been installed in the United States and Canada (97 in tributaries of Lake Superior and 65 in tributaries of Lake Michigan). Some were operated only long enough (usually 1 or 2 yr) to assess the importance of the stream for sea lamprey spawning and then discontinued if the stream was not used. About 55 barriers were operated in Lake Superior tributaries from 1953 to 1960, as a means of decreasing the sea lamprey population. After the general adoption of a chemical control method in 1958, 24 barriers on Lake Superior, 3 on Lake Michigan, and 1 on Lake Huron were operated as assessment devices to measure changes in the numbers of spawning migrants from year to year. All devices on Lake Michigan were removed after 1966 and the number of index weirs was reduced to 16 on Lake Superior (all in the United States) in 1968–70 and to 8 in 1971–78. The device in the Ocqueoc River, Lake Huron, continued to monitor the sea lamprey spawning migration in that stream, and in 1965–66, five index weirs were installed in streams tributary to Georgian Bay and northern Lake Huron in Canada.

The number was increased to eight in 1967–75, and then reduced to four in 1976–77. Only three were operated in 1978.

It is difficult to assess the influence of the barriers on the sea lamprey population. Most of the devices were not operated long enough to reduce the numbers of parasitic lampreys migrating to the lake from the streams, and the system of electromechanical barriers was never complete, even on Lake Superior; however, the barriers were effective in some areas in assessing the effects of chemical treatments on sea lamprey control.

The operation of electrical barriers, although not considered an effective method for controlling sea lamprey populations, had killed many lampreys. The effect of this reduction is not clear. It may have been beneficial, but it also could have resulted in improved spawning success by the lampreys that managed to bypass the barriers, and could have affected the lamprey ammocoetes favorably (e.g. increased the growth rate and reduced the time to metamorphosis) because of reduced competition in the river systems.

McLain et al. (1965) concluded that entire runs of adult lampreys could be prevented from reaching the spawning grounds with devices used in experimental control of sea lampreys with electricity on Lake Superior, but that an accurate appraisal of the effectiveness of the devices was impossible. The barriers did provide specimens from which valuable information was obtained on length, weight, sex composition, and time of migration of sea lampreys.

The search for a selective chemical lampricide continued as development and testing of electrical barriers progressed. About 6000 chemicals were tested at the Hammond Bay (Lake Huron) Biological Station of the U.S. Fish and Wildlife Service (listed in part by Applegate et al. 1957). Eventually 10 halogenated mononitrophenols were found that demonstrated more toxic effects on larval lampreys than on other fishes. Although all these compounds displayed selective toxicity, some were more desirable than others for field application because of their chemical and physical properties and cost. One compound, 3-trifluoromethyl-4-nitrophenol (TFM), had the best characteristics and was developed for field use. The early experimental treatments with this chemical were described by Applegate et al. (1961).

The screening of chemicals for lamprey toxicity continued after the development of TFM, and in 1963 the molluscicide Bayer 73 was found to be extremely toxic to lamprey larvae (Howell et al. 1964). Small amounts of this compound, when used with TFM, increased the toxicity of TFM without significantly affecting its selectivity for lamprey larvae. Various mixtures of the two chemicals (0.5 to 2% of Bayer 73) were used in some stream treatments, reducing the costs for chemicals by about 50%.

Chemical treatment of streams with lampricides began in the tributaries of Lake Superior in 1958, and was extended to tributaries of Lakes Michigan and Huron in 1960.

CHEMICAL CONTROL TECHNIQUE

The process of preparation for treatment and application of chemicals to the streams was described in detail by Smith et al. (1974). The procedure generally includes the following five steps.

1) The application of lampricides to a stream is preceded by intensive surveys to determine the distribution of sea lamprey ammocoetes in the stream. The survey report is the basis for determining the need for treatment and planning the application of the chemicals. It includes a map showing sea lamprey distribution, recommended application points, access roads, trails, and land ownership.

2) A bioassay with water from the stream to be treated must be carried out immediately before introduction of the lampricide — in contrast to surveys, which may be completed in advance of the treatment. The bioassay determines the minimum concentration of chemical needed to kill all sea lamprey larvae and the maximum concentration that can be used without causing significant mortalities to other fish. Originally each stream required one or more bioassays before treatment to determine concentration and application time. Later, as additional data were accumulated, many streams were treated with concentrations determined on the basis of regression curves developed from water conductivity and alkalinity measurements (Kanayama 1963).

3) Immediately before treatment the speed and volume of stream flow must be determined. In a short, simple stream, measurements of flow in cubic metres per second may be required only at the application point and near the mouth to determine differences in stream discharge. In a more complicated system, measurements may be needed at each application site, at the mouth of each tributary, and near the confluence of the stream with the lake. These measurements are used to calculate the amount of lampricide required to maintain desired concentrations. The speed of flow must be ascertained in each stream section to estimate travel time of each block of chemically treated water. Depending on the time required for treated water in each branch to reach the main stream, the starting times for the chemical feeders are set at predetermined intervals ranging from a few minutes to several hours to ensure arrival of the chemical at the proper location at the proper time to maintain the desired concentration.

4) When all other preparations for treatment are completed, a plan for the chemical application is plotted on a map of the stream system. All application sites are located, and precise starting times and application rates are determined that will maintain the desired concentration in all parts of the stream system. Analysis stations are selected for monitoring the concentration in the treated water as it moves downstream. Finally,

sites are selected for collection of lamprey larvae and monitoring fish reactions during the treatment.

5) The lampricide is introduced into the stream by accurately controllable pumping systems for the length of time required to ensure the maintenance of the minimum lethal concentration of toxicant for the full period indicated by the bioassay data. The changes in concentration are monitored (colorimetrically) to follow progress of the chemical downstream and determine whether corrective measures are required. Samples of dead and dying lampreys are collected throughout the area treated for study of species composition, age, growth, and other biological characteristics.

In addition to these five procedures, a posttreatment survey is often conducted to determine the effectiveness of a treatment.

Although the techniques for applying lampricide differ slightly in Canada and the United States, the stream treatments are effective in both countries.

Chemical Controls

LAKE SUPERIOR

After the specific lampricide TFM was developed, the Great Lakes Fishery Commission decided to place initial emphasis on the chemical control program in Lake Superior. The decision was based on two factors. First, lake trout had virtually disappeared from Lakes Huron and Michigan, but some stocks were still present in Lake Superior. It was essential that some of these fish survive for successful rehabilitation of the Great Lakes after control was achieved. Second, it seemed that the sea lamprey had not reached maximum abundance in Lake Superior and interruption of the rapid increase in numbers was considered possible.

Routine chemical treatments of streams with lampricides began in tributaries of Lake Superior in 1958, when 12 streams were treated (Smith et al. 1974). The first four treatments, two in Canada and two in the United States, were considered experimental. Ten of the 12 treatments were successful, as indicated by the few ammocoetes found during posttreatment surveys. One treatment was washed out by a severe thunderstorm and the other failed apparently because a drop in water temperature during treatment retarded the activity of the lampricide.

An additional 60 highly productive sea lamprey streams were treated in the following 2 yr, 1959–60, bringing the total number of Lake Superior streams treated to 72. Four of the 72 were retreated when it was found that significant numbers of sea lampreys had survived the first treatment. Initial treatments of all major sea lamprey producing tributaries of Lake Superior were completed in 1960. Retreatments to destroy new or reestablished populations and sea lampreys that had escaped the initial treatments began in 1961.

It was demonstrated in some large, complex rivers that it was difficult to obtain control with a single treatment, and that an accelerated treatment schedule, each year or in alternate years, was required to obtain the desired level of control.

Posttreatment studies and the Big Garlic River experiments of Manion and Smith (1978) demonstrated that a stream's capacity to produce sea lampreys varied greatly, and that rate of growth and time to metamorphosis of lampreys differed considerably within a stream and among streams. Individual ammocoetes metamorphosed within 3–3½ yr in some streams with optimum habitat (Purvis 1979), but some of the 1960 year-class were still metamorphosing after more than 18 yr in the Big Garlic River. Many streams are minor producers of sea lampreys and attracted only a few spawning adults, even during peak years of lamprey abundance. These marginal streams, when ammocoete populations were removed, often did not become reinfested for long periods, if ever. Lampricide treatments, therefore, must be scheduled to compensate for the wide variation in rates and magnitude of reestablishment.

In the 21 yr, 1958–78, 558 stream treatments (188 in Canada and 370 in the United States) were conducted on 123 tributaries of Lake Superior (Table 2). Of the 123 streams, 24 required only one treatment and 99 were treated 2 to 13 times to control reestablished sea lamprey populations. The 558 treatments involved 12 918 km of stream, a total flow of 2455 m^3/s, and almost 365 000 kg of TFM (Table 2).

Sea lamprey ammocoetes that migrate downstream from the spawning areas into bays, estuaries, and lakes in river systems become established in areas where normal control procedures are not effective. To reduce the numbers of ammocoetes reaching these areas, several streams were treated annually or every 2 yr.

A heavy granule formulation of the molluscicide Bayer 73 tested in two U.S. Lake Superior areas in 1966 as a means of destroying ammocoetes in lentic areas proved to be successful in reducing these populations. It was first used experimentally as a survey chemical in 1966, and was used throughout 1966–78 (often in conjunction with electroshockers) for surveying streams, estuaries, and lentic areas in the Great Lakes. Continuing annual treatments of relatively large areas in open water of the Canadian side of Lake Superior, where sea lamprey ammocoetes were abundant, were started in 1967 to effect control by reducing the population through general attrition from repeated treatments. These treatments were started in Batchawana Bay in 1967, in the Nipigon River in 1972, and in the Mackenzie River and Mountain Bay (Gravel River) in 1974, and were continued annually through 1978. In 1967–78, 83 treatments of estuaries, bays, and lentic areas associated with 17 streams on the Canadian side of Lake Superior were treated with the material. In the applications, 27 459 kg of Bayer 73 granules were applied over a total area of 136 ha.

LAKE MICHIGAN

The sea lamprey chemical control program with TFM

TABLE 2. Summary of streams treated or retreated and amounts of lampricides used in sea lamprey control in Lake Superior, 1958–78. (Lampricides used are in kilograms of active ingredient.)

	United States						Canada					
Year	No. of stream treatments	Total discharge at mouth (all treatments) (m^3/s)	Total stream kilometres treated	TFM (kg)	Bayer 73 (kg)		No. of stream treatments	Total discharge at mouth (all treatments) (m^3/s)	Total stream kilometres treated	TFM (kg)	Bayer 73 (kg)	
					Powder	Granules[a]					Powder	Granules
1958	10	17.5	286	2 842	0	0	2	1.6	39	105	0	0
1959	29	42.3	460	8 648	0	0	9	17.1	85	2 665	0	0
1960	15	103.4	639	23 371	0	0	11	162.3	386	24 743	0	0
1961	7	12.7	224	4 395	0	0	5	21.0	97	3 754	0	0
1962	19	44.4	589	10 392	0	0	13	137.1	510	19 174	0	0
1963	26	86.3	642	17 532	0	0	15	113.4	290	14 935	223	0
1964	25	46.4	417	8 101	36	0	15	212.3	414	26 803	354	0
1965	16	25.1	344	5 462	0	0	6	104.1	241	11 075	223	0
1966	5	13.1	161	2 907	0	4	14	90.1	283	11 880	225	0
1967	17	74.4	489	12 551	34	18	10	3.3	40	334	2	9
1968	2	9.4	156	3 445	0	3	7	23.3	200	2 835	52	4
1969	19	49.4	341	7 870	3	122	5	33.5	77	3 451	57	2
1970	10	31.5	399	4 824	8	13	11	121.1	124	15 916	352	1
1971	18	93.6	581	15 367	31	50	7	21.1	47	2 794	51	18
1972	24	65.1	314	8 103	30	58	14	56.9	270	6 320	113	2
1973	23	92.6	676	13 861	37	34	5	32.0	114	4 257	75	2
1974	18	26.2	323	4 470	11	88	5	9.9	45	920	12	4
1975	27	86.5	707	11 157	13	78	8	136.8	192	15 449	293	3
1976	17	19.0	169	3 872	2	141	8	14.8	84	1 995	31	1
1977	24	39.0	501	6 975	5	77	9	65.3	249	6 665	87	5
1978	19	60.0	644	8 193	2	11	9	40.6	69	4 475	64	1
Total	370	1037.9	9062	184 338	212	697	188	1417.6	3856	180 545	2214	52

[a] Granules used during surveys in conjunction with treatments.

was expanded to include Lake Michigan in 1960. Seven small tributaries along the north shore were treated during the time when water conditions would not permit work on Lake Superior streams. In general, the first round of treatments of Lake Michigan streams was completed by the end of 1965, but six minor lamprey producing streams along the southeast shore of Lake Michigan were not treated for the first time until April and May of 1966.

Retreatments to control reestablished sea lamprey populations were scheduled according to the individual stream's capacity to produce ammocoetes, as on Lake Superior. Some 22 Lake Michigan streams that were treated only once were not reinfested by lampreys. By 1978 most sea lamprey producing tributaries of Lake Michigan had been treated three to five times, but four rivers containing problem areas had been treated (all or in part) seven or eight times.

From 1960 to 1978, 364 treatments were conducted on 115 tributaries of Lake Michigan. The total water discharge at treatment was 1433 m^3/s, and 379 507 kg of lampricide was applied (Table 3).

LAKE HURON

The sea lamprey control program was expanded to include the Canadian waters of Lake Huron in 1960. In 1960 and 1961, all (21) of the streams tributary to Georgian Bay and the North Channel in which lampreys had been found were successfully treated, and in 1961–62, three tributaries to the United States side of the St. Marys River were treated. Because of the interest in controlling the lamprey population in Lake Michigan, and because of financial constraints, the Great Lakes Fishery Commission then terminated the program in Lake Huron in favor of treating all streams in Lake Michigan. The effect of initial treatments in Lake Huron was evidenced by an increase in rainbow trout taken at the Nicholson Dam Fishway, on the Nottawasaga River in southern Georgian Bay, and a decrease in wounding rates on rainbow trout and lake whitefish from Georgian Bay and the North Channel (A. A. Wainio, Ontario Ministry of Natural Resources, Maple, Ont., and J. J. Collins, Ontario Ministry of Natural Resources, South Baymouth, Ont., personal communication). Sea lampreys rapidly became reestablished in the treated rivers in both areas and the later effect of predation was evidenced by the increased frequency of lamprey wounds on rainbow trout and whitefish. Sea lamprey control was reinstated in Lake Huron in 1966 and thereafter continued on a regular basis.

During 1966–78, 274 lampricide treatments were made, bringing the total number to 298; they were divided among 48 streams in the United States and 48 in Canada (Table 4).

The use of granular Bayer 73 in Lake Huron for control of sea lampreys in lentic areas through the process of attrition was initiated in Canada in 1971 and continued through 1978. In the 8-yr period, 46 applications of the granular material on 76 ha required 14 657 kg of the chemical. The only areas where annual treatments with Bayer 73 were made, because of the abundant sea lamprey populations, were in the Root River (a tributary of the St. Marys River) and in the St.

TABLE 3. Summary of streams treated or retreated and amounts of lampricides used in sea lamprey control in Lake Michigan, 1960–78. (Lampricides used are in kilograms of active ingredient.)

Year	No. of stream treatments	Total discharge at mouth (all treatments) (m³/s)	Total stream kilometres treated	TFM (kg)	Bayer 73 (kg)	
					Powder	Granules[a]
1960	7	4.0	113	794	0	0
1961	26	31.0	406	11 199	0	0
1962	8	11.9	550	6 882	0	0
1963	22	41.4	563	11 397	0	0
1964	27	139.2	2 449	45 625	96	0
1965	24	91.7	1 384	28 505	14	0
1966	12	23.2	814	7 629	0	0
1967	12	39.6	666	14 118	30	0
1968	10	100.9	1 011	29 350	54	1
1969	12	80.6	801	19 167	42	62
1970	24	53.0	410	10 709	50	23
1971	24	58.8	1 349	16 844	25	70
1972	18	102.3	999	29 585	60	22
1973	21	100.4	1 283	23 513	63	43
1974	22	161.3	1 405	31 184	196	24
1975	19	27.0	336	6 884	22	0
1976	15	137.5	1 135	34 859	119	7
1977	37	114.9	1 181	27 752	99	41
1978	24	114.2	708	23 511	88	14
Total	364	1432.9	17 563	379 507	958	307

[a] Granules used during surveys in conjunction with treatments.

Marys River (Canadian side), adjacent to the St. Marys Rapids in Sault Ste. Marie. Although ammocoete populations were reduced in the St. Marys Rapids, it is so difficult to treat the entire area that only partial control is possible.

Changes in Sea Lamprey Population and Other Effects of Control

LAKE SUPERIOR

The decision of the Great Lakes Fishery Commis-

TABLE 4. Summary of streams treated or retreated and amounts of lampricides used in sea lamprey control in Lake Huron, 1960–78. (Lampricides used are in kilograms of active ingredient.)

	United States						Canada					
Year[a]	No. of stream treatments	Total discharge at mouth (all treatments) (m³/s)	Total stream kilometres treated	TFM (kg)	Bayer 73 (kg) Powder	Bayer 73 (kg) Granules[b]	No. of stream treatments	Total discharge at mouth (all treatments) (m³/s)	Total stream kilometres treated	TFM (kg)	Bayer 73 (kg) Powder	Bayer 73 (kg) Granules
1960	0	—	—	—	—	—	7	23.3	103	2 342	0	0
1961	1	0.3	23	144	0	0	14	74.0	365	16 928	0	0
1962	2	2.3	61	1 412	0	0	0	—	—	—	—	—
1966	18	24.3	703	11 550	9	0	10	10.6	204	2 495	41	0
1967	14	12.9	304	5 187	20	0	13	133.3	293	13 002	206	12
1968	4	11.3	299	5 497	15	0	11	36.6	299	8 378	130	16
1969	3	19.7	744	7 986	68	0	5	20.1	58	2 769	26	2
1970	27	58.3	499	17 921	123	0	11	21.4	195	4 350	55	21
1971	6	22.6	340	9 632	0	0	9	93.7	291	19 177	103	5
1972	12	26.5	1 339	12 273	7	44	14	96.8	262	10 862	136	10
1973	10	53.1	190	9 500	28	6	7	22.7	87	4 181	12	45
1974	13	8.2	130	2 899	8	52	9	179.3	140	2 872	13	8
1975	10	36.4	824	11 670	29	11	8	67.7	119	4 166	53	<1
1976	5	43.7	200	8 147	27	9	9	27.6	127	2 636	31	<1
1977	14	12.0	377	4 780	0	0	6	12.8	153	1 770	11	1
1978	15	47.9	360	16 725	34	0	11	26.8	56	2 206	4	<1
Total	154	379.5	6 393	125 323	368	122	144	846.7	2752	98 134	821	123

[a] No stream treatments in 1963–65.

[b] Granules used during surveys in conjunction with treatments.

TABLE 5. Number of adult sea lampreys taken at electrical barriers operated in eight tributaries along the south shore of Lake Superior, 1953–78.

	River								
Year	Betsy	Two Hearted	Sucker	Chocolay	Iron	Silver	Brule	Amnicon	Total
1953	221	371	750	—	—	—	—	—	1 342
1954	561	620	1299	1174	65	216	—	—	3 935
1955	567	587	1678	3350	183	765	—	—	7 130
1956	1553	1597	3856	6747	319	918	—	—	14 990
1957	774	7586	3506	8088	717	2757	3 969[a]	11 038	38 435
1958	1071	3418	1727	6168	401	2111	22 593	7 584	45 073
1959	1000	3990	2457	3490	257	773	19 225	980	32 172
1960	686	4222	4670	4167	310	1261	9 523	1 081	25 920
1961	1366	7498	3209	4201	2430	5052	22 478	4 741	50 975
1962	316	1757	474	423	1161	267	2 026	879	7 303
1963	444	2447	698	358	110	760	3 418	131	8 366
1964	272	1425	386	445	178	593	6 718	232	10 249
1965	187	1265	532	563	283	847	6 163	700	10 540
1966	65	878	223	260	491	1010	226	938	4 091
1967	57	796	166	65	643	339	364	200	2 630
1968	78	2132	658	122	82	1032	2 657	148	6 909
1969	120	1104	494	142	556	1147	3 374	1 576	8 513
1970	87	1132	337	291	713	321	167	1 733	4 781
1971	104	1035	485	53	1518	340	1 754	4 324	9 613
1972	146	1507	642	294	280	2574	4 121	132	9 696
1973	294	894	468	270	16	495	261	149	2 847
1974	201	489	249	17	1	117	568	270	1 912
1975	197	683	478	24	8	206	285	2 606	4 487
1976	148	229	314	10	33	199	1 085	80	2 098
1977	162	654	533	4	66	312	2 572	493	4 796
1978	185	355	974	6	26	162	794	2 310	4 812

[a] Experimental DC unit installed for testing; catch does not represent entire run.

sion to place initial emphasis on Lake Superior not only dictated that control efforts be directed first to that lake, but also that the evaluation of sea lampreys control and assessment of abundance of lampreys and other fishes be emphasized. Therefore, most of the information available on the effects of sea lamprey control on fish populations is from this lake.

As an economy measure, the number of index barriers was reduced from 24 to 16 in 1968, all in the United States; the eight barriers in Canadian streams were discontinued. This reduction was made on the premise that the Canadian barriers had rarely contributed as much as 10% of the total catch, and, in general, had shown trends in abundance similar to those in the U.S. index streams. The number of barriers was further reduced to eight in 1971, when the Scientific Advisory Committee of the Great Lakes Fishery Commission concluded that there was little to be gained by maintaining 16 barriers on Lake Superior when nearly all the vital information was being obtained from eight (Great Lakes Fishery Commission 1970).

Sea lamprey abundance in Lake Superior has been inferred from counts of upstream migrating adults at the eight electric barriers (Table 5) and from the changes in the incidence of wounded and scarred fish. Apparently sea lamprey numbers increased from sometime before 1953 to a first peak in 1958, decreased slightly in 1959 and 1960, and then reached the record high of 50 975 in 1961. Because the large rivers that produced incredibly large numbers of sea lamprey ammocoetes were not treated until 1960, a significant decrease in adult spawning-phase lampreys was not expected — and did not occur — until 1962, 4 yr after the first treatments with TFM. The numbers of spawning run sea lampreys then dropped suddenly and dramatically; only 7303 adults were captured at the eight index barriers in 1962 — a decline of 86% from the previous year. The sharp decrease left little doubt about the effectiveness of lampricide treatments and the ultimate success of the control program.

The population of sea lampreys apparently stabilized during the 4 yr following the initial sharp decline in 1962, at an average annual catch in 1962–65 of 9115 adults, or about 24% of the precontrol average catch of 38 535 in 1958–61 (Fig. 1). The number of adults captured fluctuated between 2630 and 9696, averaging 6605 for 1966–72. Finally, catches during the 6 yr from 1973 to 1978 indicated a further decline to only 8% of the precontrol average.

Control of the sea lamprey is without purpose unless

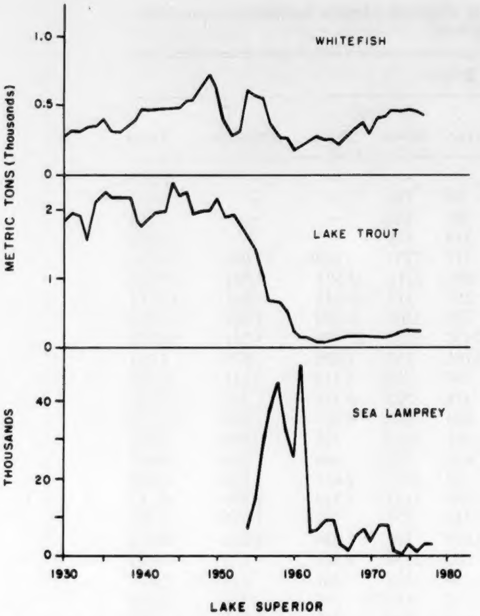

FIG. 1. Production of lake trout and whitefish in Lake Superior, 1930–77, and number of sea lampreys caught in the eight index barriers, 1954–78.

the populations of large, desirable fish such as lake trout, salmon, lake whitefish, and other valuable commercial and recreational species can be maintained or developed in harvestable numbers and sizes. Hile et al. (1951a) analyzed in detail the trends of the lake trout fishery of Lake Superior before the advent of high predation by sea lampreys. In the 20-yr period, 1933–52, preceding the decline in abundance, lake trout production remained high, averaging almost 2041 t/yr and ranging between 1588 and 2404 t/yr (Fig. 1). However, production of lake trout became unreliable as an indicator of changes in abundance after about the mid-1940s because the relation between abundance and fishing intensity was inverse (Hile et al. 1951a). Although the fishery attempted to compensate for declining abundance by increasing fishing effort, both fishing intensity and production declined after 1953.

The first stocking of lake trout in Lake Superior was in 1947. Larger plantings made in 1952–56 consisted of lake trout that were tagged or fin-clipped, as part of an experiment directed toward determining the best age for release (Buettner 1961). Nearly all fish were stocked as yearlings in later years because the experimental plants indicated this to be the best age for release.

Large-scale stocking of fin-clipped lake trout was begun after the development of the selective lampricide made sea lamprey control feasible. Annual plantings were increased to more than 1 million fish in 1958–65, and remained between 2.8 and 3.4 million in 1971–78. The total number of lake trout stocked in Lake Superior from 1958 to 1978 was 46 million — 11.1 million in Canadian waters by the Province of Ontario and 34.9 million in U.S. waters, most by the U.S. Fish and Wildlife Service.

Pycha and King (1975), who analyzed the changes in the lake trout population after 1950, showed that lakewide abundance continued downward at a rapid rate until it reached a low in 1960–61, coinciding with the peak of lamprey abundance. Lake Superior was closed to commercial lake trout fishing in 1962, and remained closed through 1978, except for a fishery (by permit in U.S. waters) to obtain the number of fish needed for biological and statistical data and a limited quota fishery begun in the early 1970s by Wisconsin. A commercial quota in Canadian waters was permitted in excess of the numbers needed for assessment. Commercial landings therefore no longer provided an index to abundance. However, R. L. Pycha (U.S. Fish and Wildlife Service, Ashland, Wisconsin, personal communication) derived a reasonably good index of abundance for two areas (the Wisconsin waters of Lake Superior and Michigan waters from Keweenaw Point to Grand Marais, Michigan) by using unweighted average catches per unit of effort (CPE) from each sample.

In Wisconsin waters the catches of lake trout of various sizes caught per 30 480 m of 11.3-cm-mesh gill net increased from a low of 244 fish in 1960 to a high of 3679 in 1970, and then declined gradually to an average of slightly less than 1700 in 1975–78. Concurrently in the Michigan area, the CPE was lowest in 1960 — 390 fish per 30 480 m of net; it increased to 4284 in 1970. Abundance continued to rise in Michigan to a peak of 6356 in 1977, then declined slightly to 5155 in 1978.

Causes of the changes in the lake trout population are not clearly understood, but after the sharp reduction of sea lamprey abundance in 1961, there was an immediate reduction of lamprey wounding rates and an obvious increase in the survival of lake trout. Certainly at a given level of lamprey control, abundance of lake trout is dependent mainly on intensity of stocking, survival of planted fish, and on mortality rate of legal-sized fish. Pycha and King (1975) concluded that the combination of limitation of fishing effort, sea lamprey control, and stocking resulted in the nearly 10-fold increase in numerical abundance of legal-sized fish and in a substantial increase in the average size of lake trout in 1961–70. They also believed that predation by sea lampreys still was a major limiting factor, but were unable to define the problems induced by hatchery rearing or stocking, especially planting in nearshore areas not formerly used as lake trout spawning grounds.

Natural spawning was successful in some areas, but in general the population of lake trout in Lake Superior through 1978 was planted fish.

After 1970, many changes further clouded the lake trout recovery picture. In Wisconsin waters abundance declined because of reduced stocking in 1964–67 and by increased exploitation thereafter (R. L. Pycha, U.S. Fish and Wildlife Service, Ashland, Wisconsin, personal communication). Similar declines in abundance have not occurred in Michigan waters from Keweenaw Point to Grand Marais, but in Whitefish Bay, at the extreme east end of Lake Superior, abundance has been reduced to about 5% of that in the Keweenaw Point–Grand Marais area. The decline was apparently caused by exploitation by sport fishing and an Indian commercial fishery on the U.S. side and a controlled commercial fishery on the Canadian side. Lake trout stocking rates were reduced beginning in 1974 and may have contributed to the decline in abundance in the later years.

The impact of sea lampreys on abundance was not nearly as drastic in lake whitefish as in lake trout, but the commercial catch of whitefish from Lake Superior did decline significantly, from an average of about 530 t in the 10-yr period, 1947–56, to 174 t in 1960 (Fig. 1; Baldwin and Saalfeld 1962). After the initial reduction in numbers of sea lampreys, commercial landings increased steadily to catches in excess of 400 t from 1970 to 1977 (M. A. Ross, Great Lakes Fishery Commission, Ann Arbor, Michigan, personal communication).

The changes in populations of important fish species in Lake Superior other than lake trout and whitefish are not easily documented, but observations and reports from commercial and sport fishermen indicate that the effect of sea lamprey control on the abundance of other species has been significant. For example, the Michigan Department of Natural Resources estimated from a postcard creel census that over 270 000 salmonids were taken by sport fishermen in 1977 (A. T. Wright, Michigan DNR, Lansing, personal communication). Lake trout contributed about 53% of the catch; rainbow trout, 18%; brown trout (*Salmo trutta*), 11%; coho salmon, 13%; and chinook salmon, 5%.

Sport fishing in Wisconsin waters of Lake Superior after the sea lamprey was controlled increased steadily from the early 1960s to a catch of almost 49 000 salmonids in 1972, declined slightly in 1973 and 1974, and then reached a peak of 51 500 fish in 1975 (G. R. King, Wisconsin DNR, Bayfield, personal communication). In 1976–78, the estimated number of salmonids caught annually was between 22 000 and 28 000, about half of the 1975 high. The reduction in numbers may have been due, at least in part, to exploitation (an Indian fishery began in Wisconsin waters in 1972). Sport fish catches in Wisconsin generally consisted of 40 to 50% lake trout; in 1978, however, that percentage was only 24. Coho salmon rose from 10% of the catch in 1976 and 1977 to 30% in 1978. (Coho salmon were not stocked in Wisconsin waters.)

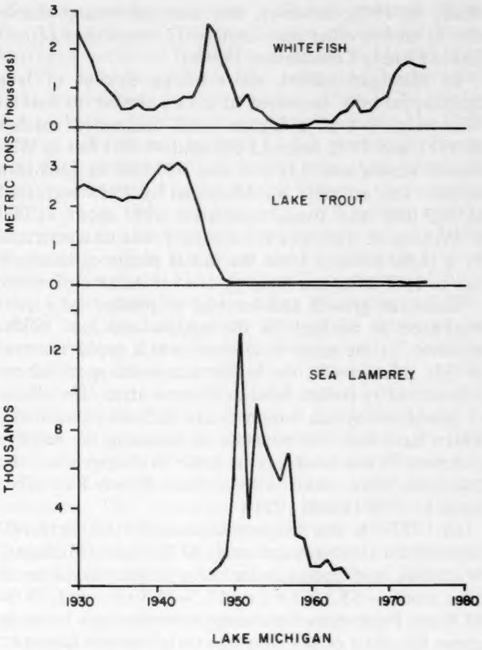

FIG. 2. Production of lake trout and whitefish in Lake Michigan, 1930–77, and numbers of sea lampreys caught in the Hibbards Creek barrier, 1947–65.

LAKE MICHIGAN

The decline and virtual disappearance of lake trout in Lake Michigan took place within a very short time (Fig. 2) and was not synchronous over the entire lake. Evidence presented by Hile et al. (1951b) showed that progression was generally from north to south and was not correlated with increased fishing intensity; some agent other than overfishing caused the lake trout to disappear and the best evidence pointed to the sea lamprey.

Inasmuch as commercial fishing for lake trout was prohibited in Lake Michigan waters, no indexes of abundance are available for 1950–68. However, an indication of numbers of all salmonids available can be inferred from Wisconsin creel census information for 1969 to 1977. Estimates of numbers of lake trout caught by sport fishermen increased rapidly from about 3000 in 1969 to a peak catch of more than 82 000 in 1974, and then decreased slightly in 1975 and 1977. Catches of lake trout and other species declined drastically in 1976; however, this decrease was probably due to factors other than changes in abundance (Great Lakes Fishery Commission 1978b).

In Michigan waters, sport fishing catches of lake trout apparently increased at a rate similar to that in Wisconsin, but at a higher level. Estimated catches in 1971 and 1972 were 43 000 and 40 000 fish in Wisconsin waters and 311 000 and 371 000 in Michigan waters. The estimate for Michigan by 1977 increased to 587 000 lake trout, compared with about 61 000 in Wisconsin. The lake trout fishery was characterized by a rapid buildup from the initial plants of hatchery fish in 1965 after sea lamprey control became effective.

Lakewide growth and survival of planted lake trout continued to be high in the middle and late 1970s; however, at the same time there was a rapid removal of fish, primarily by the highly successful sport fishery augmented by Indian fisheries in some areas. The effects of predation by sea lampreys are difficult to estimate. There have been no methods of assessing the relative numbers of sea lampreys in Lake Michigan since the last weirs were removed from three Green Bay tributaries in 1966 (Smith 1971).

In 1971–78, sea lamprey wounding rates were collected from three general areas of the lake (Michigan, Wisconsin, and Indiana) for three length categories of lake trout — 53.3–63.4 cm, 63.5–73.5 cm, and 73.6–83.6 cm. From these data some inferences can be made about the effect of sea lampreys on lake trout; however, because of variables such as changing populations of prey species, wounding rates may not closely reflect the size of the sea lamprey population in Lake Michigan.

In general, wounding rates were low (below 5%) for all size groups in the Michigan and Indiana waters of the lake (Wells 1978; Great Lakes Fishery Commission 1978b). Rates in Wisconsin remained persistently high, especially in the two larger size-groups, until 1978. Treatment with lampricides of several major lamprey producing streams tributary to Green Bay during 1977 and in the spring of 1978 doubtless was a primary reason for a reduction of wounding rates in Green Bay, and probably contributed to the decline in adjacent areas of the lake.

The lake whitefish in Lake Michigan also declined as sea lampreys became abundant, but production began to decrease in the 1930s before the invasion by the lampreys and continued downward, except for a peak in 1946–50 that was probably a result of a single highly successful year-class. The impact of sea lamprey predation and the effects of lamprey control on the lake whitefish in later years are indicated by landings in the commercial fishery (Fig. 2). The whitefish fishery reached a critical low period in the late 1950s, 4 to 5 yr after the disappearance of lake trout in Lake Michigan. Intensive exploitation caused by development of more efficient gear (the deep trap net), and the shifting emphasis of the commercial fishery from other species to whitefish, were responsible for much of the early decline (Van Oosten et al. 1946). Then, as the sea lamprey eliminated the deepwater species, they began foraging in the shallow areas, where they fed on whitefish, suckers, and other shallow-water species. After the beginning of chemical treatment of Lake Michigan tributaries for sea lamprey control in 1960, there was a steady increase in the whitefish landings, from a low of 11 t in 1957 to more than 1500 t in 1972–75 (M. A. Ross, Great Lakes Fishery Commission, Ann Arbor, Michigan, personal communication).

The State of Michigan began introducing Pacific salmon into the Great Lakes in 1966. The objectives were to introduce a large, fast-growing species that would (1) provide an abundance of sport fish for recreational fishermen, (2) reduce the large population of alewives that filled the void left by the reduction or disappearance of the ciscoes and other small species, and (3) restore the commercial fishery to a productive and economically sound industry (Tody and Tanner 1966).

In 1966–69 the States of Michigan and Wisconsin planted nearly 7.4 million coho salmon and over 2.2 million chinook salmon in tributaries of Lake Michigan (Great Lakes Fishery Commission 1974). Survival and growth of these fish were phenomenal. The coho salmon averaged over 5.5 kg in weight and some exceeded 10 kg at maturity. Some of the first chinook salmon planted, which were only 3 yr old in 1969, weighed over 15 kg.

Three major management measures — control of the sea lamprey; rehabilitation of lake trout, rainbow trout, and brown trout; and introduction of Pacific salmon — contributed to the development of a recreational fishery in Lake Michigan that is one of the finest in the world. The estimated total sport catch of the five major salmonid species in 1977 from Wisconsin and Michigan waters of the lake exceeded 3 million fish (Michigan, 2 753 000; and Wisconsin, 622 000). Pacific salmon contributed 49%, lake trout 19%, and rainbow trout and brown trout the remainder (Great Lakes Fishery Commission 1978a).

LAKE HURON

Although 24 streams were treated (21 in Canada and 3 in the United States) in 1960–62, Lake Huron was not incorporated into a continuing chemical control program until 1966; by 1968, however, all the major sea lamprey streams tributary to this lake had been treated at least once.

As in Lake Michigan, lake trout had virtually disappeared from Lake Huron by the mid-1950s (Fig. 3), but few data are available on the effect of the sea lamprey on other fish species in this lake. It is noteworthy, however, that the decline of the lake herring closely paralleled that of the lake trout. Furthermore, the commercial catch of lake whitefish in Lake Huron (excluding North Channel and Georgian Bay) declined from 1990 t in 1931 to less than 95 t in 1942. Although

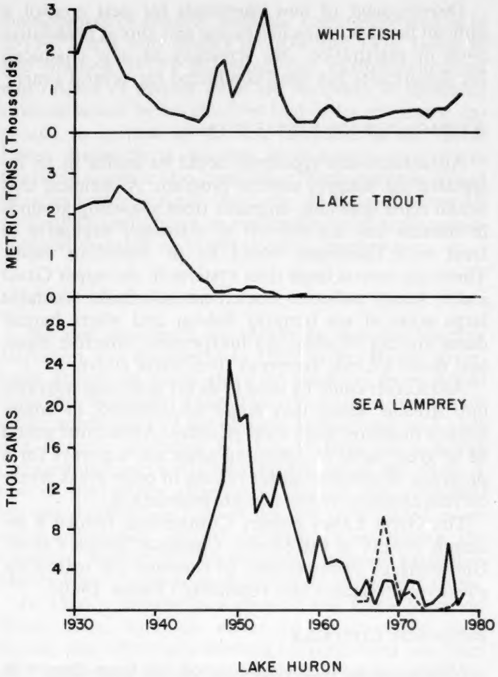

FIG. 3. Production of lake trout and whitefish in Lake Huron, 1930–77, and numbers of sea lampreys caught in the Ocqueoc River in the United States, 1947–77, and the Kaskawong, Blue Jay, Still, and Naiscoot–Harris rivers in Canada, 1965–77.

the whitefish was heavily exploited, beginning in 1930, by highly efficient new deep trap nets (Van Oosten et al. 1946), predation by the sea lamprey was probably at least partly responsible for the decline. A very successful 1943 year-class resulted in catches of about 1500 t in 1947 and 1948 but high mortality of this year-class, attributed to sea lamprey predation, resulted in a continued low level of whitefish abundance after the 1942 low (Smith 1968).

After the Great Lakes Fishery Commission was formed, management agencies agreed to rehabilitate Lake Huron with splake (hybrid brook trout, *Salvelinus fontinalis* × lake trout) rather than lake trout, hoping that the early maturity of the splake would accelerate rehabilitation of fish stocks in the presence of the remaining sea lamprey population (Great Lakes Fishery Commission 1966). The Province of Ontario began planting splake as early as 1966. The first plants were exploratory and were not selected fish. In 1969, 35 000 young splake of the F_5 generation, selected to mature rapidly and to occupy the areas and depths of the lake formerly used by lake trout, were planted. Plantings of selected splake continued in Ontario through 1978. The U.S. Fish and Wildlife Service planted splake in Michigan waters of Lake Huron in 1970–72, and then in 1973 introduced both lake trout and backcrosses (lake trout female × male splake). After 1973, splake and backcross plantings were discontinued on the U.S. side of Lake Huron because of fish disease problems with the splake brood stock, but lake trout plantings were maintained (Great Lakes Fishery Commission 1975). From 1969 to 1978, over 10.9 million splake, lake trout, and backcrosses were introduced into Lake Huron (4.1 million in Canada and 6.8 million in United States waters; Great Lakes Fishery Commission 1978b). Only a few splake have been taken by commercial fishermen in Canadian waters. The splake appeared to have dispersed throughout the lake instead of remaining in the areas of planting. Sport fisheries for splake have developed in certain local areas — e.g. in the rapids and power plant tailraces at Sault Ste. Marie.

There is no authorized commercial fishery for lake trout or splake in Michigan but creel census figures for 1971 indicated that about 2800 were caught by sport fishermen. The estimated catch increased to almost 50 000 fish in 1976 and almost 128 000 in 1977 (A. T. Wright, Michigan DNR, Lansing, personal communication). Unfortunately, an Indian commercial fishery in St. Martins Bay and other United States waters of northern Lake Huron appears to be a serious threat to lake trout stocks.

It has been necessary to use fish other than lake trout to monitor sea lamprey wounding rates in Lake Huron because stocks of large lake trout have not had time to develop.

Approximately 1.6 million coho and chinook salmon were planted in Lake Huron in 1968 and 1969, all in the United States waters (Great Lakes Fishery Commission 1974). The first mature coho salmon and precocious chinook salmon ("jacks") entered streams in 1969 in Canadian and U.S. waters. It was believed that the salmon would be less vulnerable than lake trout to lamprey predation because of their pelagic habitat and fast growth. Unfortunately this belief was not supported. Lamprey scarring rates were about 85% on mature coho salmon and 62% on the 2-yr-old chinook salmon — a dramatic contrast with Lake Superior, where the scarring of adult coho salmon was less than 1%, and Lake Michigan, where scarring rates on both species were less than 5%.

Salmon plantings by the Michigan Department of Natural Resources continued in 1970–78; 8 million chinook salmon and 5.3 million coho salmon were stocked through 1978 (Great Lakes Fishery Commission 1978b). Lamprey wounding of chinook salmon remained high (26.8%) until 1972, then apparently as results of the sea lamprey treatment program began to take effect on sea lamprey populations, the wounding rate dropped to 7 and 8.6% in 1973–74, 5% in 1975, and 2.4% in 1976 (Great Lakes Fishery Commission 1976).

Development of Other Methods of Control

The extraordinary amount of damage inflicted on the fisheries of the Great Lakes by the invasion of the sea lamprey has resulted in one of the largest and most intensive efforts to control a vertebrate predator ever attempted. Successful suppression of the parasite and rehabilitation of the Great Lakes into an area for production of high-value food fishes and the development of the natural resources for maximum recreational use are milestones in fish population manipulation and management.

Unfortunately, the sea lamprey control program is based almost entirely on the use of chemicals. A comprehensive program of studies of the effect of the lampricides on other organisms, terrestrial and aquatic, and in recent years a strict protocol of registration-oriented research to investigate their efficacy, mutagenic, carcinogenic, and teratological effects, proved that the chemicals when used by professional applicators are environmentally safe. However, increasing costs, potentially limited supplies, and other considerations have caused increasing concern about reliance on a single technique. At the Great Lakes Fishery Commission's Annual Meeting in June 1970, L. P. Voigt, then Chairman, voiced his concern and encouraged increased attention to the use of permanent barriers, both for sea lamprey control and anadromous fish management.

L. H. Hanson (Great Lakes Fish. Comm., Ann Arbor, MI, Appendix VI, December 1970, mimeograph) examined the literature on various control methods used in other pest control programs, and suggested that some of these techniques were feasible and suitable for use in the sea lamprey control program.

Essentially, the Great Lakes Fishery Commission and its two control agents have since that time been committed to a program of integrated control — an evolving system that combines suitable techniques in a compatible manner to eliminate or reduce unwanted populations to levels below those causing economic or other damage.

An integrated sea lamprey control program can be divided into five general parts — the use of chemical lampricides, attractants and repellents, and biological, genetic, and mechanical controls.

CHEMICAL LAMPRICIDES

The application of lampricides constitutes only a temporary, restricted, and expensive method. The chemicals must be introduced into the environment at periodic intervals on a continuing basis because sea lampreys in the lake can enter the stream to spawn after the stream has been treated, and it is impossible to eradicate sea lampreys in some stream systems. There may be little difference between a high degree of control and elimination of the population, but because of the limitations of chemical control, elimination probably is impossible.

Development of new chemicals for pest control is difficult because of the increasing and almost prohibitive costs of registration. No screening of new chemicals for lampricides has been conducted for several years.

ATTRACTANTS AND REPELLENTS

Attractants and repellents could be useful in an integrated sea lamprey control program. A chemical that would repel spawning migrants from spawning grounds in streams that are difficult or extremely expensive to treat with chemicals would be of enormous value. There are several large river systems in the upper Great Lakes where pollution abatement will make available large areas of sea lamprey habitat and where barrier dams are not feasible. An inexpensive, effective repellent could exclude lampreys from these rivers.

Attractants could be used to direct spawning migrants into streams where they could be collected, or where control measures were most effective. Attractants would be of great value in collecting adult sea lampreys for a program of sterilization for release in other areas where current chemical techniques are impractical.

The Great Lakes Fishery Commission funded a research project at the Monell Chemical Senses Center, University of Pennsylvania, to continue the search for effective attractants and repellents (Teeter 1980).

BIOLOGICAL CONTROLS

Most work on biological controls has been done with insects — sometimes with highly successful results. Much of the information developed should apply in a general way to attempts to control sea lampreys biologically. However, little effort has been expended toward developing biological controls. McLain (1952) studied the parasites in sea lampreys from northern Lake Huron, but found no natural parasites that might be developed for lamprey control. At about the same time, in the initial search for control measures, consideration was given to the possibility of a natural predator — specifically the American eel, *Anguilla rostrata* (H. A. Loeb, U.S. Fish. Wildl. Service, Great Lakes Fishery Investigation, 1951, unpublished data; Perlmutter 1951) — but the use of these animals appeared to be impractical. The American eel has been present in large numbers in Lake Ontario, but has had no apparent effect on the lamprey population.

Other possibilities for biological controls, such as competitive displacement by other species, physiological alteration of the sea lamprey to prevent metamorphosis or induce neoteny, or manipulating habitat to make it unsuitable, have been discussed, but development of such methods will require greater funding and specialized expertise than is now available to the control agencies.

GENETIC CONTROLS

The use of genetic controls has been directed toward development of sterility methods. Laboratory studies in 1971–73 and field studies in 1974 and 1975 (Hanson and Manion 1978) suggested that chemosterilization and release of mature male sea lampreys in spawning streams would be an effective tool in an integrated approach to control of the sea lampreys in the Great Lakes. Research to develop immunologic procedures for sterilization is also continuing. Such methods would be advantageous since they rely on natural materials and would not require as much expensive registration-oriented research as would control chemicals.

MECHANICAL CONTROLS

The first dam built specifically to stop sea lamprey migration was completed in 1957 in the Harris River, Lake Huron, to block entry by lampreys from Bright Lake into Basswood Lake. The concrete structure, built under supervision of the Ontario Department of Lands and Forests, produced a 1.5-m vertical fall and was incorporated into a highway bridge across the river. A row of steel plates attached to the top and overhanging the downstream side of the dam was added as an extra precaution against lampreys surmounting the structure. Sea lamprey ammocoetes, although present in Harris River, have never been found above this dam.

In 1966 a fishway in a dam on the Black Sturgeon River, Lake Superior, about 16 km from the river mouth, was effectively blocked by vinyl-lined jute bags of mixed concrete. In addition, steel plates were installed on the top stoplogs of each of the seven sections of the dam, forming an overhanging lip, to act as an upstream barrier to adult sea lampreys during periods of high water. Sea lamprey ammocoetes have not been found above the structure; consequently the length of stream requiring lampricide treatment has been reduced from 81.6 to 16 km, the length of time required to treat the river has been reduced from 6 to 3 d, and the degree of treatment effectiveness has increased significantly.

In the fall of 1971, a barrier dam to stop spawning-run sea lampreys was constructed on rock-filled timber cribwork on the Echo River, Lake Huron, about 1.6 km above Echo Lake. There were problems with flood damage and holes in the structure, requiring repairs in 1972–73. The dam was resurfaced in 1976 with concrete and backfilled with slag and gravel, and it is now believed to function as a sea lamprey barrier.

The French River, which drains Lake Nipissing and flows into Georgian Bay, is a complex network of interconnecting waterways about 80 km long. Sea lampreys are established in some areas of this system, but not above the Wanapitei River. To prevent infestation of the upper French River, two rapid-type falls were modified by blasting to develop lamprey barriers.

Dennys Dam, located on the Saugeen River, a tributary to Lake Huron, at Southampton, Ontario, is a multipurpose dam constructed in 1969–70. The primary purpose of the dam is to prevent the upstream migration of spawning sea lampreys. The inclusion of a lamprey trap and a fish ladder-trap in the dam, operated and maintained annually by Ontario Ministry of Natural Resources, allows for the capture of adult sea lampreys as well as for the capture and upstream passage of spawning rainbow trout. The cost of the dam was $264,000, shared equally by the Canadian federal and provincial governments. Benefits of this dam to the sea lamprey control program have been great since sea lampreys have failed to reestablish themselves in the river. When some 80 km of the main stream and tributaries of this river were treated with lampricide in 1971, the cost of chemicals alone was $70,500.

Additional impetus was given to the barrier dam program in June 1971, when the Great Lakes Fishery Commission formed Canadian and United States task forces to provide information on the number of sea lamprey producing streams that have existing dams which constitute barriers, the number with existing dams that could be modified to provide barriers to sea lampreys, and the number of streams on which installation of dams could provide sea lamprey control. The reports of the national task forces were presented in December 1971 at an Interim Meeting of the Great Lakes Fishery Commission (A. L. McLain et al., Great Lakes Fish Comm., Ann Arbor, MI, Appendix XX, 1971, mimeograph; Great Lakes Fishery Commission, Ann Arbor, MI, Appendix XXI, 1971, mimeograph).

The importance of the barrier dam program was reiterated by the Commission in a policy statement adopted December 1, 1975, entitled, "The role of dams in an integrated sea lamprey control program":

> The Commission strongly endorses the installation of barrier dams as part of an integrated control program. Direct participation by the Commission is limited except for possible financial assistance to States and Province to construct devices designed specifically for sea lamprey control. The Commission also strongly urges the Great Lakes States and the Province of Ontario, in concert with their respective federal governments and in cooperation with this Commission, to initiate an active barrier dam program to enhance the efficiency and effectiveness of the sea lamprey control program in the waters of the Great Lakes. The Commission recognizes that action by the States and Province must be taken within the constraints imposed by laws or regulations of the individual agency.

With the expectation that funds for barrier dams would become available in fiscal year 1978, the Commission approved, in June 1977, a barrier dam program for sea lamprey control with funds designated to grant up to 100% of the actual costs of acquisition of a site and of the design and construction costs of a barrier dam.

NEED FOR INTEGRATED SEA LAMPREY CONTROL

It is essential that the Great Lakes Fishery Commission develop a program for integrated control of the sea lamprey to reduce the nearly complete dependence on chemical lampricides. Research on many aspects of an integrated program will have to be completed by agencies with specialized expertise. Neither the Commission nor its sea lamprey control agents can afford to develop the capabilities to investigate pathogens, to alter or replace hereditary material, to change the physiological response, or to investigate new and imaginative ideas that may be forthcoming. Solicitation of specific research projects for assistance and funding is essential to the development of a fully integrated sea lamprey control program.

Future of Sea Lamprey Control in the Great Lakes

The unique control measures used under direction of the Great Lakes Fishery Commission have met with significant success. The control program in the upper three lakes has suppressed the numbers of sea lamprey effectively and permitted the redevelopment and reestablishment of stocks of high-value fishes and the development of the fish resources for maximum recreational use.

Although sea lamprey control has met with considerable success in Lakes Superior, Michigan, and Huron, there are still major problems to be solved and important decisions to be made before the most effective and economical production of maximum numbers of important food and sport fishes can be expected.

The presence of sea lamprey ammocoetes in areas where present control measures cannot be used, or are ineffective, continues to be a major problem. Larvae in estuarine and lentic areas at the mouths of tributaries, backwaters, oxbows, beaver flowages, and in stream-bed spring areas sometimes survive treatments because of dilution and poor circulation of the lampricide. Generally, sea lampreys in these areas are being controlled, however, by modifying the treatment procedure to include application of lampricide into the mouths of tributaries, spot treatment of problem areas where practical, and in some streams, more frequent treatment to prevent movement of larvae into inaccessible areas.

There are, however, large areas, such as Nipigon River, St. Marys River, and the St. Clair River, where sea lampreys have been found and where our present technology is not adequate to reduce the numbers of larvae and to prevent the production of parasitic-phase animals. Some examples of major problems are given below.

The Nipigon River system includes large expanses of Helen Lake, the lower river below Helen Lake, and a large section of Nipigon Bay that contains sea lamprey ammocoetes. Selected sections have been treated with granular Bayer 73 from 1971 to 1978, apparently with no significant reductions in the populations. The St. Marys River between Lakes Superior and Huron contains a sparse population of sea lamprey ammocoetes above the locks at Sault Ste. Marie, a large number of larvae in the rapids areas adjacent to the ship canals, and significant numbers of ammocoetes as far as 37 km downstream from the compensating gates at the upper end of the Sault Rapids. The only attempts at control of the St. Marys River sea lampreys have consisted of yearly treatments of the ammocoete habitat between the bottom of the rapids and the Canadian ship canal with Bayer 73 granules. The numbers of lampreys collected fluctuate annually and ammocoetes have been eradicated in some areas; however, it is difficult to apply the lampricide to all infested areas.

A small number of sea lamprey larvae are present in the upper St. Clair River below the outlet of Lake Huron, but the size of the infestation would indicate that there is no significant contribution to the parasitic population from this area.

Another serious problem for the sea lamprey control program is the increase in usable sea lamprey habitat created by increased emphasis on pollution abatement and habitat enhancement for salmonids — specifically, the removal of dams and the improvement or construction of efficient fishways over or around barriers. The Commission and the control agents are encouraging the incorporation of lamprey control devices wherever possible. Some examples of river systems that can become major problems for lamprey control are the St. Louis River in Minnesota; the Fox and Sheboygan Rivers in Wisconsin; the Grand, St. Joseph, Kalamazoo, and Saginaw Rivers in Michigan; and the Spanish River in Ontario.

A need for better methods to evaluate the effects of control efforts by monitoring sea lamprey abundance and fish populations is evident. At present, only Lake Superior has a reliable index to lamprey numbers, based on counts of spawning migrants at eight electric barriers and on changes in wounding rates on lake trout. Six weirs were operated on northern Lake Huron and Georgian Bay tributaries, but catches from these barriers have not been proven to represent the sea lamprey numbers in the lake except in the Georgian Bay area, where there was a marked decrease in lamprey numbers from 1968 to 1978 (Table 1).

No index of actual sea lamprey numbers in Lake Michigan has been available since the electric barriers on Green Bay tributaries were discontinued in 1966.

Developmental and feasibility studies with small, mechanical traps placed in strategic locations below dams and natural barriers were begun in 1975 and continued through 1978 (R. J. Schuldt, U.S. Fish Wildl. Serv., Marquette Sea Lamprey Control Station, Marquette, MI, 1976, unpublished data). These devices, fished consistently in the optimum locations, seem to give a reliable indication of the relative number of spawning migrants and a good sample to monitor changes in biological characteristics from year to year.

Permanent fishing sites are being established on each of the upper three lakes, and as a good data base is established, catches at these sites will provide a reliable index to the adult sea lamprey populations.

A good data series exists on the changes in abundance of lake trout in Lake Superior, and the effect of sea lampreys on the population is being observed through lake trout catches, changes in wounding rates, and determination of mortality rates from experimental gillnet fishing (Pycha 1980; Lawrie and MacCallum 1980). There were no similar efforts on Lakes Michigan and Huron until 1976 (Wells 1980).

A lake trout technical committee was formed in January 1976 under the sponsorship of the Great Lakes Fishery Commission's Lake Michigan Committee. The goal of this committee is to develop a unified interagency assessment program that will provide a scientific data base for managing the lake trout stock on a lakewide basis. The information from this program combined with the lamprey wounding data being consolidated by the Great Lakes Fishery Laboratory at Ann Arbor, Michigan, should provide the necessary insight into the effects of sea lamprey predation and sea lamprey control on fish stocks in Lake Michigan.

Emphasis on monitoring fish stocks lakewide in Lake Huron has been limited in the past. There is, however, an excellent series of data for 1964–78 on wounding of lake whitefish along the south shore of Manitoulin Island (Spangler 1970). Some information on lamprey wounding of chinook salmon is collected each year by the Michigan Department of Natural Resources, but there is no organized program to detail the effect of sea lamprey control on the fish populations of Lake Huron.

The success of the sea lamprey control program is now dependent almost entirely on the use of the chemical lampricide, TFM. The price of TFM more than doubled from a low of $2.55 per pound in 1968–69 to $6.49 per pound in late 1978. In addition, some of the basic components of the lampricides are petroleum-based derivatives and could present supply problems as the world oil situation worsens. During the oil boycott of 1974, the suppliers of TFM alerted the Commission to potential problems, and in fact, set a maximum limit on how much could be produced.

There is also a continuing problem with registration of chemicals as required by the Environmental Protection Agency (EPA) in the United States. At the Interim Meeting in December 1970, the Commission was apprised of the original notice of cancellation of the registered use of TFM for control of sea lampreys in the Great Lakes. An extension of registration was granted in 1971 on the basis of a tentative research protocol developed to establish tolerances. The final data to complete the original research protocol were submitted to EPA in early 1976. In July and mid-August 1978, EPA amended the guidelines for registration of fishery compounds — a change that may or may not affect present TFM registration, but probably will affect reregistration when required. Similar problems are occurring with registration of Bayer 73.

In addition to the above problems, the introduction of substantial quantities of any chemical compound into the environmental is open to question, regardless of safety. Certainly if the Commission's agents continue to rely on lampricides, and make only token efforts to develop other methods of control, they are not responsibly addressing their responsibilities.

The final and perhaps most important question for sea lamprey control is, "How much sea lamprey control is enough?" Eradication of a predator species in such large bodies of water seems impractical if not impossible, and maintenance of the final level of suppression achieved may have to be continued indefinitely (Smith 1971). The question of what level of control will meet the demands of the Great Lakes community has been discussed informally many times, but as yet no serious attempts have been made to consider the benefits of sea lamprey control either biologically or from a socioeconomic viewpoint.

The Great Lakes Fishery Commission has as one of its major objectives the reestablishment of self-sustaining lake trout populations. This goal was reiterated in a policy statement, "Position on lake trout rehabilitation," adopted on June 14, 1976. The level of sea lamprey control necessary to attain this objective has not been determined and may or may not have yet been attained. Although some natural reproduction of lake trout occurs in certain areas, notably areas of Lake Superior, the present control and stocking programs, combined with mortality, harvest, and unknown environmental factors have not established the desired level of natural reproduction. It is conceivable that with increased stocking of lake trout, Pacific salmon, and other desirable fishes, a less than optimum sea lamprey control program with a reduction in lampricide and funding could satisfy the demands of management agencies. Brinser et al. (1968) estimated that the cost–benefit ratio of lamprey control at the 85% level in Lake Superior was significant, ~$5 in net benefits to the sport and commercial fisheries for each $1 spent on sea lamprey control or to produce hatchery fish for planting. The study was completed before the introduction of Pacific salmon and the unprecedented boom in the sport fishery, and is not relevant now. However, it did indicate a favorable cost–benefit ratio with an annual net benefit of about $2 million.

Inasmuch as Talhelm (1979) stated that the current sport fishing value for Michigan waters of the Great Lakes is about $250 million and the value of commercial fishing is $2–$3 million, we believe that similar figures for the Province of Ontario and other Great Lakes States, if available, would show that the total value of Great Lakes fisheries at the 1978 level of sea lamprey control and fish stocking rates was atonishingly high.

Unfortunately, little effort has been made through 1978 to answer the question of how much lamprey control would be most productive, either from a cost-benefit or a biological standpoint. As Lawrie (1970) indicated, a sea lamprey program indefinitely maintained is a social service and must yield a return worthy of the investment.

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Applegate, V. C. 1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 35: 237 p.

Applegate, V. C., J. H. Howell, A. E. Hall Jr., and M. A. Smith. 1957. Toxicity of 4,346 chemicals to larval lampreys and fishes. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 207: 157 p.

Applegate, V. C., J. H. Howell, J. W. Moffett, B. G. H. Johnson, and M. A. Smith. 1961. Use of 3-trifluormethyl-4-nitrophenol as a selective sea lamprey larvicide Great Lakes Fish. Comm. Tech. Rep. 1: 35 p.

Applegate, V. C., J. H. Howell, and M. A. Smith. 1958. Use of mononitrophenols containing halogens as selective sea lamprey larvicides. Science 127(3294): 336–338.

Applegate, V. C., and B. R. Smith. 1951. Sea lamprey spawning runs in the Great Lakes, 1950. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 61: 45 p.

Applegate, V. C., B. R. Smith, A. L. McLain, and M. Patterson. 1952. Sea lamprey spawning runs in the Great Lakes, 1951. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 68: 37 p.

Baldwin, N. S., and R. W. Saalfeld. 1962. Commercial fish production in the Great Lakes 1867–1960. Great Lakes Fish. Comm. Tech. Rep. 3: 166 p.

Braem, R. A., and W. J. Ebel. 1961. A back-pack shocker for collecting lamprey ammocetes. Prog. Fish-Cult. 23: 87–91.

Brinser, A., L. L. Smith Jr., H. C. Frick, and F. E. J. Fry. 1968. An economic evaluation of sea lamprey control and lake trout restoration in Lake Superior. Great Lakes Fish. Comm., Ann Arbor, MI.

Buettner, H. J. 1961. Recoveries of tagged hatchery-reared lake trout from Lake Superior. Trans. Am. Fish. Soc. 90: 404–412.

Crowe, W. R. 1975. Great Lakes Fishery Commission history, program, and progress. Great Lakes Fish. Comm., Ann Arbor, MI. 23 p.

Great Lakes Fishery Commission. 1958, 1966, 1970, 1974, 1975, 1976, 1978b. Annual reports of the Great Lakes Fishery Commission, Ann Arbor, MI.

1978a. Minutes of Annual Meeting of Lake Michigan Committee, March 1978. Great Lakes Fish. Comm., Ann Arbor, MI. Appendix XI, p. 69.

Hanson, L. H., and P. J. Manion. 1978. Chemosterilization of the sea lamprey (*Petromyzon marinus*). Great Lakes Fish. Comm. Tech. Rep. 29: 15 p.

Hile, R., P. H. Eschmeyer, and G. F. Lunger. 1951a. Status of the lake trout fishery in Lake Superior. Trans. Am. Fish. Soc. 80: 278–312.

1951b. Decline of the lake trout fishery in Lake Michigan. U.S. Fish Wildl. Serv. Fish. Bull. 52: 77–95.

Howell, J. H., E. L. King Jr., A. L. Smith, and L. H. Hanson. 1964. Synergism of 5,2′-dichloro-4′-nitrosalicylanilide and 3-trifluoromethyl-4-nitrophenol in a selective lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 8: 21 p.

Hubbs, C. L., and T. E. B. Pope. 1937. The spread of the sea lamprey through the Great Lakes. Trans. Am. Fish. Soc. 66: 172–176.

Kanayama, R. K. 1963. The use of alkalinity and conductivity measurements to estimate concentrations of 3-trifluormethyl-4-nitrophenol required for treating lamprey streams. Great Lakes Fish. Comm. Tech. Rep. 7: 10 p.

1970. The sea lamprey in the Great Lakes. Trans. Am. Fish. Soc. 99: 766–775.

Lawrie, A. H., and W. MacCallum. 1980. On evaluating measures to rehabilitate lake trout (*Salvelinus namaycush*) of Lake Superior. Can. J. Fish. Aquat. Sci. 37: 2057–2062.

1953. Sea lamprey spawning: Wisconsin and Minnesota streams of Lake Superior. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 97: 36 p.

Loeb, H. A., and A. E. Hall Jr. 1952. Sea lamprey spawning: Michigan streams of Lake Superior. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 70: 68 p.

MacKay, H. H. 1951. Progress Report of Sea Lamprey Investigations in Ontario 1951. Minutes of Great Lakes Trout Comm. and Great Lakes Sea Lamprey Comm. 1951: 24–44.

Manion, P. J., and B. R. Smith. 1978. Biology of larval and metamorphosing sea lampreys, *Petromyzon marinus*, of the 1960 year class in the Big Garlic River, Michigan, Part II, 1966–72. Great Lakes Fish. Comm. Tech. Rep. 30: 35 p.

McLain, A. L. 1952. Diseases and parasites of the sea lamprey, *Petromyzon marinus*, in the Lake Huron basin. Trans. Am. Fish. Soc. 81: 94–100.

McLain, A. L., B. R. Smith, and H. H. Moore. 1965. Experimental control of sea lampreys with electricity on the south shore of Lake Superior, 1953–60. Great Lakes Fish. Comm. Tech. Rep. 10: 48 p.

Morman, R. H. 1979. Distribution and ecology of lampreys in the Lower Peninsula of Michigan, 1957–75. Great Lakes Fish. Comm. Tech. Rep. 33: 59 p.

Perlmutter, A. 1951. An aquarium experiment on the American eel as a predator on larval lampreys. Copeia 1951: 173–174.

Purvis, H. A. 1979. Variations in growth, age at transformation, and sex ratio of sea lampreys reestablished in chemically treated tributaries of the Upper Great Lakes. Great Lakes Fish. Comm. Tech. Rep. 35: 36 p.

Pycha, R. L. 1980. Changes in mortality of lake trout (*Salvelinus namaycush*) in Michigan waters of Lake Superior in relation to sea lamprey (*Petromyzon marinus*) predation, 1968–78. Can. J. Fish. Aquat. Sci. 37: 2063–2073.

Pycha, R. L., and G. R. King. 1975. Changes in the lake trout population of southern Lake Superior in relation to the fishery, the sea lamprey, and stocking, 1950–70. Great Lakes Fish. Comm. Tech. Rep. 28: 34 p.

Smith, B. R. 1971. Sea lampreys in the Great Lakes of North America, p. 207–247. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London and New York.

Smith, B. R., J. J. Tibbles, and B. G. H. Johnson. 1974. Control of the sea lamprey (*Petromyzon marinus*) in Lake

Superior, 1953–70. Great Lakes Fish. Comm. Tech. Rep. 26: 60 p.

SMITH, S. H. 1964. Status of the deepwater cisco populations of Lake Michigan. Trans. Am. Fish. Soc. 93: 155–163.

1968. Species succession and fishery exploitation in the Great Lakes. J. Fish. Res. Board Can. 25: 667–693.

SPANGLER, G. R. 1970. Factors of mortality in an exploited population of whitefish, *Coregonus clupeaformis*, in northern Lake Huron, p. 515–529. *In* C. C. Lindberg and C. S. Wood [ed.] The biology of coregonid fishes. Univ. of Manitoba Press, Winnipeg, Man.

STAUFFER, T. M. 1961. Distribution of sea lamprey ammocetes in Lake Michigan tributaries of the Upper Peninsula of Michigan, 1955–59. Mich. Dep. Conserv. Misc. Publ. 14: 21 p.

STAUFFER, T. M., AND M. V. HANSEN. 1958. Distribution of sea lamprey ammocetes in Michigan tributaries of Lake Superior. Mich. Dep. Conserv. Inst. Fish. Res. Misc. Publ. 11: 25 p.

TALHELM, D. R. 1979. Fisheries: dollars and cents. Water Spectrum (U.S. Army Corps Eng.) 11(1): 8–16.

TEETER, J. H. 1980. Pheromone communication in sea lampreys (*Petromyzon marinus*): implications for population management. Can. J. Fish. Aquat. Sci. 37: 2123–2132.

TIBBLES, J. J. 1959. Preparations for lamprey control in Lake Huron. Prog. Rep. Fish. Res. Board Can. 1: 22–27.

TODY, W. H., AND H. A. TANNER. 1966. Coho salmon for the Great Lakes. Fish Manage. Rep. Mich. Dep. Conserv. 1: 38 p.

VAN OOSTEN, J., R. HILE, AND F. OBES. 1946. The whitefish fishery of Lakes Huron and Michigan with special reference to the deep-trap-net fishery. U.S. Fish Wildl. Serv. Fish. Bull. 50: 297–394.

WELLS, L. 1978. Sea lamprey wounding rates on lake trout, Lake Michigan, September–October, 1978. Report of the Interim Meeting, November 1978, Great Lakes Fish. Comm., Ann Arbor, MI, p. 29–30.

1980. Lake trout (*Salvelinus namaycush*) and sea lamprey (*Petromyzon marinus*) populations in Lake Michigan, 1971–78. Can. J. Fish. Aquat. Sci. 37: 2047–2051.

Sea Lamprey (*Petromyzon marinus*) in the Lower Great Lakes[1]

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Sea lamprey (*Petromyzon marinus*) are established in each of the several discrete areas in the St. Lawrence River system between Lake Huron and the Moses–Saunders Power Dam (160 km below Lake Ontario) except for the Niagara River between Niagara Falls and Lake Ontario. However, chemical lampricide treatments are being used to control these populations only in Lake Ontario. Experimental introductions of trout and salmon in Lake Ontario between 1968 and 1971 were not successful. Survival was limited and the number of sea lamprey attack marks on the fish that did mature was very high. After the first round of lampricide treatments of most sea lamprey producing tributaries in 1972, survival of fish improved and lamprey attacks declined. Studies are being completed to determine the desirability of including Oneida Lake in the treatment schedule to prevent recruitment of sea lampreys from this area to Lake Ontario and to improve the fish populations of Oneida Lake. Treatment of Lake Champlain also is being studied by management agencies concerned with its fisheries. Lake St. Clair and Lake Erie and connecting waters, the Finger Lakes, and the St. Lawrence River below Lake Ontario do not appear to have sea lampreys in the numbers necessary to cause unacceptable levels of predation on fish populations and are not being considered for inclusion in the Great Lakes Fishery Commission control program at this time.

Key words: sea lamprey, predation, abundance, history, Erie, Ontario, Oneida, Finger Lakes, Champlain

Pearce, W. A., R. A. Braem, S. M. Dustin, and J. J. Tibbles. 1980. Sea lamprey (*Petromyzon marinus*) in the Lower Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1802–1810.

La grande lamproie marine (*Petromyzon marinus*) est établie dans chacune des nombreuses aires discontinues du réseau du fleuve Saint-Laurent, entre le lac Huron et le barrage hydroélectrique Moses–Saunders (160 km en aval du lac Ontario), à l'exception de la rivière Niagara entre les chutes Niagara et le lac Ontario. Cependant, ce n'est que dans le lac Ontario qu'on utilise des lampricides chimiques dans le but de contrôler ces populations. Les peuplements expérimentaux de truites et de saumons dans le lac Ontario entre 1968 et 1971 n'ont pas réussi. La survie était limitée et le nombre de marques laissées par les lamproies sur les poissons qui avaient atteint la maturité était très élevé. Après une première ronde de traitements aux lampricides de la plupart des tributaires produisant des grandes lamproies marines en 1972, la survie des poissons s'améliora et les attaques par la lamproie diminuèrent. On est à terminer des études entreprises dans le but de déterminer s'il était désirable d'inclure le lac Oneida dans le programme de traitement afin d'empêcher le recrutement, dans le lac Ontario, de grandes lamproies marines provenant de cette région et d'améliorer les populations de poissons du lac Oneida. Les organismes de gestion des pêches du lac Champlain étudient eux aussi le traitement de ce lac. Les lacs Sainte-Claire et Érie, de même que les eaux qui les relient, les lacs Finger et le fleuve Saint-Laurent en aval du lac Ontario ne semblent pas avoir suffisamment de grandes lamproies marines pour créer des niveaux inacceptables de prédation chez les populations de poissons. On ne songe donc pas pour le moment à inclure ces régions dans le programme de contrôle de la Commission des pêcheries des Grands Lacs.

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MOVEMENT of the sea lamprey (*Petromyzon marinus*) into Lakes Huron, Michigan, and Superior, and the subsequent series of biological changes initiated by the destruction of valuable fish stocks and the effects on fish not directly attacked by the parasite resulted in concerted action by the various agencies concerned with Great Lakes fisheries. In 1956, the Great Lakes Fishery Commission, established by a treaty between Canada and the United States, began the task of coordinating efforts to formulate and implement a program to eradicate or minimize sea lamprey populations in the Great Lakes. The two agents of the Commission for lamprey control are the U.S. Fish and Wildlife Service and the Department of Fisheries and Oceans of Canada. The history and methodology of the control program in the three upper lakes have been described by Smith et al. (1974) and Smith and Tibbles (1980).

Emphasis of the sea lamprey control program was directed first to Lake Superior and later to Lakes Michigan and Huron to save the remnant populations of lake trout and to restore the badly damaged commercial fisheries as quickly as possible. Little effort was directed toward Lakes Ontario and Erie until 1963. In this report we summarize the history and control of sea lampreys in the two Lower Great Lakes, their connecting waters: the Finger Lakes and Oneida Lake, tributary to Lake Ontario through the Oswego River, and Lake Champlain, tributary to the lower St. Lawrence River.

St. Lawrence River

The St. Lawrence River is the natural outlet of the Great Lakes (Fig. 1) and one of the largest rivers in North America. Sea lamprey ammocoetes have not been found in tributaries of the upper St. Lawrence River from Lake Ontario to the Moses–Saunders Power Dam (a distance of 160 km). A limited population of sea lampreys in the river proper attack northern pike (*Esox lucius*) and other fish (Dunning et al. 1978); however, the present magnitude of sea lamprey predation is not considered a major fisheries management problem.

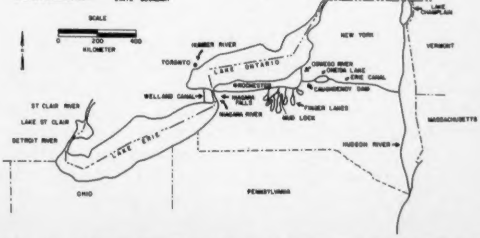

FIG. 1. Lower Great Lakes and waters associated with sea lamprey origin and distribution.

Whether or not sea lampreys in the St. Lawrence River originate from the eastern basin of Lake Ontario or result from spawning directly in the river is not known. It is doubtful that ammocoetes produced in the river would contribute significantly to the Lake Ontario population because of the strong downstream currents. Present treatment technology will not permit sea lamprey control in the St. Lawrence River.

Lake Champlain

Although Lake Champlain (surface area 1129 km^2) is much smaller than Lake Ontario, there are many similarities. It is one of the largest lakes in North America and is sometimes referred to as the sixth Great Lake. It is an international waterway shared by the States of New York and Vermont and the Province of Quebec, and drains, via the Richelieu River, into the St. Lawrence River near Montreal. Historically, it contained lake trout (*Salvelinus namaycush*) and Atlantic salmon (*Salmo salar*), which became extinct about the same time as Lake Ontario's populations (Parsons 1973). In recent years, stocking of lake trout, rainbow trout (*Salmo gairdneri*), and Atlantic and landlocked (Sebago) salmon maintained populations of these fish without sea lamprey control.

Surveys of Lake Champlain tributaries indicate that there is an abundance of sea lamprey ammocoetes in many streams, and trout and salmon are heavily parasitized. Fisheries scientists are accumulating data on wounding and scarring of fish by lampreys and on the growth and survival of fish stocks to help concerned management agencies to decide whether or not sea lamprey control will be a part of the fisheries' management programs for Lake Champlain. This determination will include socioeconomic and environmental concerns as well as biological factors.

Lake Ontario

Lake Ontario, the smallest of the five Great Lakes, is the 14th largest freshwater lake in the world with a surface area of about 19 500 km^2. Although eutrophication caused considerable chemical and biological changes in the shallow areas of the eastern end and lakewide embayment areas, Lake Ontario (mean depth 86 m) is considered oligotrophic. The Upper Great Lakes supply about 80% of Lake Ontario's water through Niagara River (Fig. 1); the remainder is provided by about 600 tributaries. A few tributaries, the Trent, Moira, Black, Salmon, Oswego, and Genesee rivers, have large drainage basins, but most others have small drainage areas. Niagara Falls was a barrier to fish and sea lamprey movement from Lake Ontario into the other Great Lakes until 1829 when the Welland Ship Canal was completed between lakes Ontario and Erie.

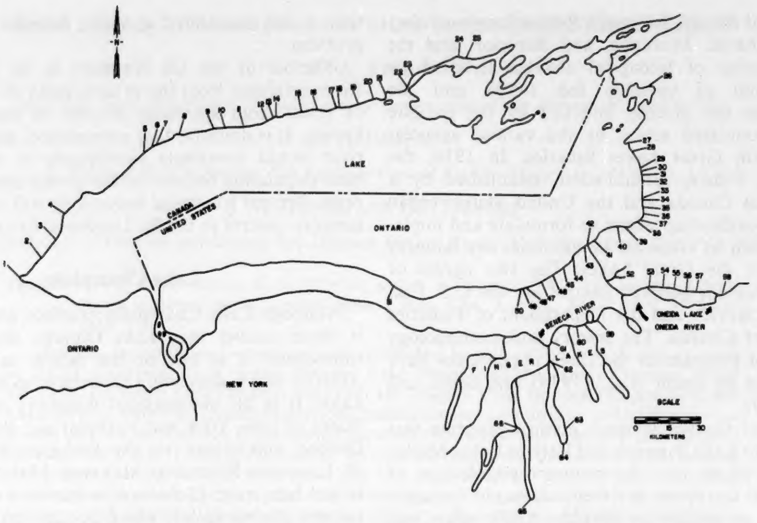

FIG. 2. Canadian and United States tributaries of Lake Ontario and the Oswego, Seneca, and Oneida rivers and Lakes Oneida, Seneca, and Cayuga containing sea lamprey larvae: Canada: 1 Ancaster Cr., 2 Bronte Cr., 3 Oakville Cr., 4 Credit R., 5 Rouge R., 6 Duffin Cr., 7 Carruthers Cr., 8 Lynde Cr., 9 Oshawa Cr., 10 Farewell Cr., 11 Bowmanville Cr., 12 Wilmot Cr., 13 Graham Cr., 14 Port Britain Cr., 15 Gage Cr., 16 Cobourg Br., 17 Grafton Cr., 18 Shelter Valley Br., 19 Lakeport Cr., 20 Salem Cr., 21 Proctors Cr., 22 Smithfield Cr., 23 Mayhew Cr., 24 Moira R., and 25 Salmon R.; United States: 26 Black R., 27 Stony Cr., 28 South Sandy Cr., 29 Skinner Cr., 30 Lindsey Cr., 31 Blind Cr., 32 Little Sandy Cr., 33 Deer Cr., 34 Salmon R., 35 Grindstone Cr., 36 Snake Cr., 37 Sage Cr., 38 Little Salmon R., 39 Butterfly Cr., 40 Catfish Cr., 41 Rice Cr., 42 Oswego R., 43 Ninemile Cr., 44 Sterling Cr., 45 Blind Sodus Cr., 46 Red Cr., 47 Wolcott Cr., 48 Sodus Cr., 49 Third Cr., 59 First Cr., 51 Northrup Cr., 52 Black Cr., 53 Big Bay Cr., 54 Scriba Cr., 55 Dakin Cr., 56 Cold Spring Br., 57 Hall Br., 58 Fish Cr., 59 Carpenter Br., 60 Cold Spring Br., 61 Crane Br., 62 Yawger Cr., 63 Salmon Cr., 64 Cayuga Lake Inlet, 65 Catharine Cr., and 66 Keuka Lake Outlet.

The origin of the sea lamprey in Lake Ontario is controversial. Fothergill's (undated) checklist identifies the possible presence of sea lampreys about 1817, and some believe they are a relict species from the last Pleistocene glaciation (Christie 1973). The first authenticated record of sea lampreys in the Great Lakes was taken from Duffin Creek, a Canadian tributary to Lake Ontario, in 1835 (Lark 1973). Aron and Smith (1971) and many others support the theory that sea lampreys may have entered Lake Ontario from the Hudson River via New York's Erie Canal sometime after the early 1820s (Fig. 1). Other possible routes of entry are the St. Lawrence River or the headwaters of the Susquehanna River drainage immediately south of New York's Finger Lakes (Smith 1972).

Early Studies of Sea Lamprey Distribution and Abundance

The Province of Ontario, in 1950, issued a circular of available information on sea lampreys and emphasized the importance of locating streams with spawning runs. In the 1950s, a number of Canadian studies were initiated to gather additional data on the status of sea lampreys in Lake Ontario. A weir was installed on Bronte Creek (Fig. 2) in 1952 to capture adult sea lampreys for information on abundance and biological characteristics. Questionnaires were sent monthly to commercial fishermen in 1954 requesting information on the incidence of sea lamprey marks on their fish catches.

From 1959 to 1962, personnel from the Fisheries Research Board of Canada investigated the extent of sea lamprey use of the Welland Ship Canal. All tributaries of the canal were examined for ammocoete habitat and spawning gravel. Certain areas were checked with electric shockers for ammocoetes, but no lampreys of any species were captured (Dodge 1963). In 1963, 230 Canadian streams were surveyed between the Niagara and Salmon rivers; sea lamprey larvae were in 17. Of an additional 158 Canadian tributaries of Lake Ontario and the upper St. Lawrence River surveyed from 1964 to 1978, 8 contained sea lampreys (Fig. 2).

The U.S. Fish and Wildlife Service made an initial investigation of streams along the U.S. shore of Lake Ontario in 1965 to provide information for planning subsequent surveys. These surveys, which began in 1969, were to determine the presence or absence of sea lampreys in Lake Ontario tributaries of New York. Of 135 tributaries examined, 18 (all east of Rochester, New York) contained sea lamprey ammocoetes (Fig. 2). In 1970–78, eight additional streams were found to contain larval sea lampreys, only one being west of Rochester.

In summary, by 1978, sea lampreys were found in 51 of 620 tributaries of Lake Ontario and the St. Lawrence River surveyed (Fig. 2). Sea lampreys were not found in tributaries of the St. Lawrence River from Lake Ontario to the Quebec border. In many Lake Ontario tributaries, natural and man-made barriers, stream desiccation, high water temperatures, urban pollution, and marginal sea lamprey spawning and larval rearing conditions combine to limit the number of streams used by sea lampreys, as well as the density of ammocoetes.

The most prolific areas of sea lamprey recruitment to Lake Ontario are between Toronto and the western reaches of the Bay of Quinte in Ontario and from Oswego east to Stony Point in New York. A total of 35 sea lamprey producing streams of Lake Ontario were in these mostly rural areas which are less influenced by urban and industrial pollution. A significant portion of the area has gradually changed from open farm and pastureland to woodland. The abundance of spawning and larval habitat within these clear, shaded streams, coupled with a source of groundwater originating from wooded, hilly country, make these streams well suited for sea lamprey production. Successful United States and Canadian pollution abatement programs will continue to increase the amount of desirable stream habitat for sea lamprey spawning and ammocoete nursery areas.

Effects of Sea Lamprey Predation on Fish Stocks (Precontrol)

The major changes in the fish stocks of Lake Ontario since the early settlers found an abundance of such highly desirable species as the Atlantic salmon, lake trout, and lake whitefish (*Coregonus clupeaformis*) were well documented by Christie (1974). Although commercial fishing catch data are not always an accurate record of species abundance, they are the only early quantitative information and most of the changes in Lake Ontario fish stocks were inferred from these catches. Baldwin and Saalfeld (1962) and Christie (1973) documented the history of the depletion and eventual extinction in 1950 of lake trout.

Reports of sea lamprey attacks on Lake Ontario fish stocks appeared about 1890 (Dymond et al. 1929; Parsons 1973). Dymond did not consider sea lampreys a threat to lake trout production. Christie (1973) believed that if sea lamprey predation was a factor in the extinction of lake trout, it was only after overharvest by commercial fishing had severely depleted the population. A brief history of Lake Ontario's fishery here will place the question of sea lamprey control in perspective.

Parsons (1973) documented the collapse of the Atlantic salmon fishery by 1840–50 and their extirpation by 1900. He noted that Lake Ontario may have contained the largest freshwater Atlantic salmon population in the world. Loss of suitable spawning streams because of construction of mill dams, tannery pollution, and siltation caused by intensive lumbering and construction was probably the major cause of the salmon's demise. Sea lamprey predation was not considered a factor in the loss of the salmon stocks.

Burbot (*Lota lota*), lake trout, and lake whitefish were scarce by 1909, but increased in numbers by the 1920s. Burbot, as well as native lake trout, were extinct by 1950, whereas the whitefish population collapsed by 1960 (Christie 1973). Herring and chubs or coregonines, which consisted primarily of lake herring (*Coregonus artedii*), shortnose cisco (*C. reighardi*), bloater (*C. hoyi*), and kiyi (*C. kiyi*); were important commercial and forage species. Their collapse also caused major changes in the species composition in the lake and the associated commercial fishery (Christie 1973). Coregonines were replaced by rainbow smelt (*Osmerus mordax*) (Greeley 1939) and alewife (*Alosa pseudoharengus*) (Aron and Smith 1971). The two species provide most of the excellent forage base for large predator species now present in Lake Ontario.

In the early 1950s, limited experimental lake trout stockings by the Province of Ontario and the State of New York in Lake Ontario produced excellent survival of fish to a length of about 38–45 cm, but there was little survival of larger trout. Monofilament (newly introduced) gill nets set for lake whitefish harvested many small lake trout, and sea lampreys preyed heavily on larger fish. Between 1965 and 1972, Ontario stocked large numbers of sockeye (kokanee) salmon (*Oncorhynchus nerka*) fry and eyed eggs in Lake Ontario and tributaries without success.

The State of Michigan, in the mid-1960s, initiated a very successful stocking program for coho salmon (*O. kisutch*) and chinook salmon (*O. tshawytscha*) to develop a sport fishery in Lake Michigan. Because of the success of the program in Michigan, New York in 1968 introduced 25 000 coho salmon into the Salmon River system of Lake Ontario. Between 1968 and 1971, New York stocked about 517 000 coho salmon and 310 000 chinook salmon, and the Province of Ontario introduced 3 371 000 kokanee fry, 446 000 coho, and 45 000 splake (hybrid brook trout, *Salvelinus fontinalis* × lake trout) in Lake Ontario before the start of sea lamprey control. However, survival was extremely poor. The average number of sea lamprey attack marks on the few surviving coho and chinook salmon in the spawning runs in the Salmon River, New York, was 10 and 13 per fish, respectively (Great Lakes Fishery Commission 1968–71).

Only limited Canadian and no United States commercial fishing for salmon and trout was allowed in Lake Ontario from 1968 to 1973, and commercial fishing was not considered a factor in the unsuccessful attempt to develop a salmonid fishery. It was evident to most fisheries' scientists that sea lamprey predation on stocked salmonids was probably a major limiting factor in developing a fishery. The failure of salmonid stockings in the absence of sea lamprey control prompted the Lake Ontario Committee of the Great Lakes Fishery Commission to recommend that sea lamprey control be extended to Lake Ontario.

Sea Lamprey Control Program

Sea lamprey control began in Lake Ontario with the treatment of 23 streams along the Canadian shore in 1971 and 20 streams on the United States side in 1972. In 1973, the Canadian sea lamprey control unit assumed responsibility for treatment of all tributaries of Lake Ontario, including those in New York. Personnel from the U.S. Fish and Wildlife Service and the New York Department of Environmental Conservation continued surveys to define sea lamprey ammocoete distribution and to assess the effects of control in New York waters. The methodology of control is the standard method of lampricide application used in the upper lakes and is described by Smith (1971) and Smith et al. (1974).

During the 8-yr period, 1971–78, a total of 105 lampricide treatments were performed on 46 Lake Ontario tributaries. Of the 51 streams known to contain sea lampreys, 5 (Northrup and Red creeks and Black, Oswego, and Moira rivers) have not been treated. The Oswego River is the only untreated stream suspected of contributing significantly to parasitic stocks in Lake Ontario. Thirty-six streams were treated two or more times and 10 were only treated once. During these treatments, about 39 550 kg of the lampricides 3-trifluoromethyl-4-nitrophenol (TFM) and 5,2′-dichloro-4′-nitrosalicylanilide (Bayer 73) were applied to 1960 km of stream at a combined discharge of 236 m^3/s.

Effects of Sea Lamprey Control

The effects of lampricide treatments in Lake Ontario are difficult to assess. Weirs and traps were not installed in tributaries to measure the abundance of sea lampreys before the advent of chemical control. The only information available is annual counts of spawning run sea lampreys captured by dip nets at night in the Humber River, at the base of a dam in Toronto in 1968–78. Briefly, the catches by this rather inefficient method ranged from 1221 in 1968 to 6848 in 1975, which did not coincide with the expected reduction in numbers of adult sea lampreys after the initiation of chemical control. The average length of the adult sea lampreys from the Humber River increased from about 41 cm in 1968 to 47 cm in 1977. No ammocoetes have been found in the river.

Portable traps fished at the base of dams or other barriers to capture adult sea lampreys have potential to provide reliable information on abundance and biological characteristics. Site selection for these traps has been in progress since 1978 (Braem and Moore 1979).

Personnel from the New York Department of Environmental Conservation counted sea lamprey nests in designated areas of some spawning streams in 1971–78 to determine if these data could be correlated with changes in numbers of spawning sea lampreys (Great Lakes Fishery Commission 1971–78). These data are inconclusive. Annual ammocoete stream surveys are also continuing, but this information is used primarily to schedule stream treatments.

A more conclusive and encouraging indication of the success of the sea lamprey control program is the significant decline in the number of scars and wounds on salmonids. From 1971 to 1978, the percentage of age II+ coho and chinook salmon bearing sea lamprey attack marks declined from almost 100 to about 50, and the number of wounds or scars per fish decreased from 13 to less than 1 (Great Lakes Fishery Commission 1971–78).

Increased stocking rates could have increased the number of fish in relation to the number of sea lampreys and perhaps decreased the percentage of attack marks without a decrease in the number of lampreys. However, the average size of coho and chinook salmon increased dramatically, and large numbers of age III+ and older chinook salmon began to appear indicating increased survival of larger and older fish. The mean length and weight of age II+ fall-run coho salmon increased from about 61 cm and 2.4 kg in 1971 to 75 cm and 5 kg in 1978. In these same years, chinook salmon increased in average size from 72 cm and 4.1 kg to 86 cm and 7.8 kg. By 1978, age III+ and older chinook salmon were common and ranged from 13.6 kg to over 18 kg (Great Lakes Fishery Commission 1971–78).

Lake trout were successfully reintroduced into Lake Ontario in 1973. Increased stocking to about 1.5 million lake trout a year by 1979 will probably provide the best future sea lamprey control assessment data through wound-scar counts and lake trout growth-survival information. Such data should be available by 1980–81 when large numbers of lake trout will have reached spawning age.

Sea lamprey control obviously is a necessary part of any program to develop and maintain what will soon be a 100-million-dollar salmonid sport fishery in Lake Ontario (Pearce 1978). The current level of control in this lake is considerably less than in lakes Superior, Michigan, and Huron, and it appears that there are one or more major uncontrolled sources of parasitic sea lampreys entering the lake that must be identified and eliminated.

Oswego River Drainage

The Oswego River system is the largest and most complicated tributary to Lake Ontario except for the Niagara River. It includes the Seneca River–Finger Lakes and the Oneida River–Oneida Lake complex (Fig. 2) and is connected to the Niagara and Mohawk rivers by the Erie Canal. An extensive study of all parts of the Oswego River system by several agencies is continuing to determine the magnitude of their contribution of parasitic sea lampreys to Lake Ontario.

OSWEGO RIVER

The Oswego River proper runs from the confluence of the Oneida and Seneca rivers to Lake Ontario, a distance of about 40 km. Most of its length is impounded by eight shipping locks and dams. A channel depth of about 3.7 m is maintained. The river does not appear suitable for sea lamprey production, and its locks and dams are almost certainly a deterrent to sea lamprey spawning migrations.

Surveys of the Oswego River and its tributaries indicate that there are no sea lamprey ammocoetes in the river proper, but that one small tributary, Black Creek (Fig. 2), contains some ammocoetes, and its treatment was recommended to the Great Lakes Fishery Commission for the 1980 field season.

SENECA RIVER AND FINGER LAKES

The large watershed of the Oswego River system contains the several lakes comprising the Finger Lakes. Only two of the lakes, Cayuga and Seneca, are known to contain sea lampreys. Moderate to abundant populations of sea lamprey ammocoetes have been confirmed by surveys in Cayuga Inlet, and Yawger and Salmon creeks, tributary to Cayuga Lake (Chiotti 1976), and in two Seneca Lake tributaries, Catharine Creek and Keuka Lake Outlet. Surveys of the other lakes and the Seneca River demonstrated that some lampreys were present in three small tributaries of the river — Crane, Cold Spring, and Carpenter brooks (Fig. 2).

Both Cayuga and Seneca lakes contain salmonids, including lake trout, brown trout (*Salmo trutta*), and rainbow trout and an abundance of sea lampreys. The trout populations are augmented or maintained by an effective stocking program. The incidence of sea lamprey attacks on lake trout has increased significantly since 1959. The number of both wounds and scars on individual lake trout in the 650- to 699-mm-length group rose from an average of 1.81 during 1959–64 to 3.60 in 1979. On large fish (700–749 mm), the average number of attack marks per fish reached 4.68 in 1979 (Jolliff et al. 1980). In addition, Jolliff and Neth (1980) state that evidence indicates that the Seneca Lake native lake trout population, a major source of brood stock for New York State, is declining. However, Youngs (1972) could not demonstrate any significant effect of lamprey-induced mortality on the lake trout population of Cayuga Lake.

An experiment has been proposed by the New York Department of Environmental Conservation for sea lamprey control on the two lakes using lampricides in the tributaries of Seneca Lake and a combined barrier and weir on Cayuga Inlet. Such an experiment would not only demonstrate the effectiveness of two methods, but document the effects of reduced sea lamprey numbers on the salmonid populations.

The origin of sea lampreys in Cayuga and Seneca lakes is unknown. Studies using electrophoresis techniques are underway to determine if there are genetic differences between these lampreys and those in Lake Ontario and the other Great Lakes. Results may indicate whether or not the Finger Lakes are contributing sea lampreys to the parasitic population of Lake Ontario. Fyke net sampling in the fall of 1976 and spring of 1977 did not indicate any movement of recently metamorphosed lampreys downstream from the Finger Lakes. Nets were fished in the vicinity of Mud Lock below Cayuga Lake from October 20 to December 4, 1976, and from March 24 to April 25, 1977; three adult sea lampreys were captured.

On the basis of present information, it would appear that the Finger Lakes are not contributing significantly to sea lamprey populations in Lake Ontario. Therefore, until more definitive data are available, the Great Lakes Fishery Commission is not directly concerned with sea lamprey control in these lakes.

ONEIDA RIVER AND ONEIDA LAKE

Oneida Lake is the largest lake entirely within the State of New York and is the nearest to Lake Ontario of any lake in the Oswego River system. A large sea lamprey population is known to be present in this lake. Sea lamprey ammocoetes were found in six Oneida Lake tributaries — Big Bay and Fish creeks, and Dakin, Scriba, Cold Spring, and Hall brooks. Fish Creek has about 112 km of excellent habitat and supports a large number of sea lamprey ammocoetes.

Fyke nets were fished for sea lampreys in the Oneida River below Caughdenoy Dam, about 6.4 km downstream from Oneida Lake, from October 20 to December 4, 1976, and March 24 to April 25, 1977. In the fall of 1976 the river was at or near flood stage with high velocities, making netting very difficult. In the spring of 1977 the flow was even higher throughout the period, in contrast to the Seneca River where water levels were near normal and fishing was good. A total of 12 metamorphosed sea lampreys were captured at Caughdenoy, 6 between November 15–28 and 6 between March 27–April 6. One adult was captured on March 26.

The capture of any young sea lampreys under such adverse conditions probably indicates a major movement of newly metamorphosed sea lampreys from

Oneida Lake into Lake Ontario via the Oneida and Oswego rivers (Fig. 2). Sea lamprey control was proposed by the control agents, and the Commission assigned an ad hoc committee to evaluate the proposal. The committee determined that there was not adequate information on lake trout or other fish stocks in Lake Ontario to assess properly the effects of sea lamprey control in Oneida Lake on populations of sea lampreys and salmonids in Lake Ontario (Pearce 1978). Additional data also are needed to determine the effects of sea lamprey control on Oneida Lake fish stocks. Data will be available by 1980–81 to assess an experimental sea lamprey control project on the Oneida Lake system. The results of treatments of the tributaries of Lake Oneida on Lake Ontario's sea lamprey and salmonid populations, particularly lake trout, will have to be very dramatic and obvious to justify the inclusion of the Oneida system as a permanent part of the control program in the judgment of the ad hoc committee of the Great Lakes Fishery Commission.

Niagara River

Extensive surveys in the Niagara River, and the Niagara Bar, a large, delta-like area in Lake Ontario off the mouth of the river, have not produced sea lamprey larvae. As water quality improves in the river and chemical conditions improve in the surface sediments of the Niagara Bar, both areas will be potential new sources of sea lamprey larvae.

Lake Erie and Lake St. Clair

Lake Erie is the fourth largest of the five Great Lakes with a surface area of over 25 700 km^2. The shallow (maximum depth 64 m), warm waters of the lake apparently are of less than optimum quality for sea lampreys and only a few streams support spawning runs. The population of lampreys has never been large and predation on fish stocks has never been serious.

Historically, Lake Erie supported a commercial fishery for lake trout and lake whitefish. Native lake trout are now extinct and lake whitefish drastically reduced (Christie 1974). Blue pike (*Stizostedion vitreum glaucum*), once very abundant in Lake Erie, are now considered extinct. Rainbow smelt, yellow perch (*Perca flavescens*), and walleye (*S. vitreum vitreum*) presently are three of the more important fish species (Great Lakes Fishery Commission 1971–79). In recent years coho salmon, chinook salmon, rainbow trout, and brown trout were stocked with some success. Survival of lake trout recently introduced in the eastern basin is encouraging and this species may soon be successfully reestablished in Lake Erie.

There are no records of sea lampreys in Lake Erie before 1921 (Dymond 1922). As noted earlier, Niagara Falls, between lakes Erie and Ontario, constituted a barrier to sea lamprey migration until the Welland Ship Canal was constructed in 1829. It was not until 1932 that the first spawning sea lamprey run was noted in Pine River (Creaser 1932), and in 1934 sea lampreys were observed in the Huron River, a tributary of the Lake Erie–Lake St. Clair system (Shetter 1949). Surveys of 368 tributaries of Lake Erie between 1957 and 1978 indicated that there are only 14 streams (Catfish, Big Otter, Big, Potters, and Youngs creeks and the Grand River in Canada; Delaware, Cattaraugus, Canadaway, Crooked, Raccoon, and Conneaut creeks and the Grand and Sandusky Rivers in the United States) that contain sea lamprey ammocoetes.

Concern by fisheries' agencies over the possible establishment of sea lampreys in Lake St. Clair was recorded as early as 1950, when small lamprey traps were fished in Little River at Tecumseh, Ontario (1950 Report of the Great Lakes Sea Lamprey Committee, unpublished data). Forty-six tributaries to the Detroit River, Lake St. Clair, and the St. Clair River were surveyed between 1964 and 1978). Small populations of sea lampreys were found in the Thames River in Ontario and in the St. Clair River and two of its tributaries, Pine and Black rivers, in Michigan.

Recent sea lamprey wound and scar data on Lake Erie salmonid stocks confirm that sea lamprey predation is not a serious problem at this time (Great Lakes Fishery Commission 1971–79). The primary reason for low sea lamprey populations in lakes Erie and St. Clair is probably the lack of good spawning and ammocoete habitat in the tributary systems. Another factor may be the limited number of desirable prey fish available to the sea lamprey.

These factors limiting sea lamprey populations in Lakes Erie and St. Clair may soon change: as United States and Canadian pollution abatement programs continue to improve stream habitats, and as the salmonid management programs become more successful, there will be an increase in desirable prey fish. Sea lampreys from eastern basin streams of Lake Erie may be contributing to the Lake Ontario population. If true, then any increase in the production of sea lampreys in the Lake Erie system could have a major impact on Lake Ontario.

At the 1979 annual meeting of the Great Lakes Fishery Commission, the Lake Erie Committee recommended that the above concerns be addressed and a decision made within 2 yr on whether or not to begin sea lamprey control on lakes Erie and St. Clair. Regardless of the decision, sea lamprey monitoring must be a part of future fisheries' management programs on the two Great Lakes.

Role of Sea Lamprey Management in the Lower Great Lakes Area

There are several discrete areas in or associated with the lakes Erie and Ontario drainage basin. Each has its own specific fisheries' management problems, and as sea lampreys are present in all sectors except perhaps the Niagara River below the falls, the need for lamprey control should be established for each area. If sea lampreys are relatively new to these waters, gaining access after the opening of the Erie Canal about 1825, they may have been at least a contributing factor to the loss of several desirable fish species. However, if sea lampreys are indigenous, they have lived compatibly as parasites with Atlantic salmon and lake trout.

An intensive program to control sea lampreys in Lake Ontario was initiated in 1971 because prior experimental introductions of lake trout, coho salmon, and chinook salmon indicated that the high levels of sea lamprey-induced mortality would prevent development of an acceptable fishery. The dramatic decrease in the number of fish bearing lamprey attack marks and the number of wounds or scars per fish and the increase in size of fish after the effects of sea lamprey control became apparent in 1973 strongly suggest that the numbers of sea lampreys must be controlled if a viable and valuable sport fishing industry is to be established in Lake Ontario.

The relatively high number of sea lamprey attack marks still observed on trout and salmon in Lake Ontario after 8 yr of lamprey control, when compared with records from the three Upper Great Lakes, strongly suggest that significant recruitment to the parasitic population in the lake continues. Present information from surveys and other sampling indicates that Oneida Lake is a probable source, and chemical treatment of its tributaries has been recommended by the two sea lamprey control agents of the Great Lakes Fishery Commission.

The data assembled by various agencies indicate that of the other areas of the Lower Great Lakes and St. Lawrence River included in this report, Lake St. Clair, Lake Erie, and the St. Lawrence River below Lake Ontario have populations of sea lampreys, but the magnitude of predation does not at this time present major fisheries' management problems. No plans are being formulated to include these areas in the Great Lakes Fishery Commission's sea lamprey control program.

Two of the Finger Lakes, Cayuga and Seneca, have moderate populations of sea lampreys and considerable parasitism on lake trout and rainbow trout exists. However, there is evidence that this area is not contributing to the parasitic sea lamprey populations in Lake Ontario and there are no immediate plans for control.

The last area, Lake Champlain, does contain a population of sea lampreys preying on its salmonids. This lake lies outside the convention area of the Great Lakes Fishery Commission and is, therefore, not of concern to that body or its agents. Data are being accumulated by the fisheries' agencies concerned with management and a plan is being formulated to initiate control independently if proven desirable.

The role of sea lamprey control in the management of the fisheries of each one of the separate areas of the Lower Great Lakes must be carefully evaluated by the concerned management agents. A major challenge to fisheries' scientists is to determine the need for sea lamprey control, and the methods and level of control most desirable for each area on the basis of social, economic, environmental, and biological considerations. The future of sea lamprey control in the Great Lakes may be determined on how judiciously fisheries' managers, administrators, and others include all interests in decision making, planning, and operation of sea lamprey management.

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ARON, W. I., AND S. H. SMITH. 1971. Ship canals and aquatic ecosystems. Science 174: 13–20.

BALDWIN, N. S., AND R. W. SAALFELD. 1962. Commercial fish production in the Great Lakes 1967–1970. Great Lakes Fish. Comm. Tech. Rep. 3: 10 p.

BRAEM, R. A., AND H. H. MOORE. 1979. Sea lamprey control in the United States, p. 45. *In* Annu. Rep. Great Lakes Fish. Comm. (Append. V), Ann Arbor, MI.

CHIOTTI, T. J. 1976. Distribution of sea lamprey ammocoetes in tributaries and estuaries of Cayuga, Seneca and Keuka lakes. New York State Dep. Environ. Conserv. Rep. pp. 1, 2, 8–11.

CHRISTIE, W. J. 1973. A review of the changes in the fish species composition of Lake Ontario. Great Lakes Fish. Comm. Tech. Rep. 23: 65 p.

1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Board Can. 31: 827–854.

CREASER, C. W. 1932. The lamprey *Petromyzon marinus* in Michigan. Copeia 1932: 157.

DODGE, D. P. 1963. Survey of the Welland Ship Canal for sea lampreys (*Petromyzon marinus*). J. Fish. Res. Board Can. Manuscr. Rep. Ser. (Biol.) 745: 31 p.

DUNNING, D. J., J. T. EVANS, AND M. J. TANBY. 1978. Baseline biological studies preparatory to the assessment of winter navigation on the St. Lawrence River. State Univ. New York, Proj. 2106-1-6141. Syracuse Univ., a Res. Foundation of State Univ. New York College of Environ. Sci. Forestry. 144 p.

DYMOND, J. R. 1922. A provisional list of the fishes of Lake Erie. Univ. Toronto Stud., Biol. Ser., Pub. Ont. Fish Res. Lab. 4: 57–73.

DYMOND, J. R., J. L. HART, AND A. L. PRITCHARD. 1929. The fishes of the Canadian waters of Lake Ontario. Univ. Toronto Stud., Biol. Ser. 33: 1–35.

FOTHERGILL, C. (n.d.). Memoirs and illustrations of natural history in various parts of the British Empire (Clendenan volume). Roy. Ont. Mus. (call number R.B., M.S. F661' No. 3). (Information from this paper taken from Lark 1973.)

GREAT LAKES FISHERY COMMISSION. 1968–71, 1971–78. Lake Ontario Committee annual reports. *In* Annu. Rep. Great Lakes Fish. Comm., Ann Arbor, MI.

1971–79. Lake Erie Committee annual reports. *In* Annu. Rep. Great Lakes Fish. Comm., Ann Arbor, MI.

GREELEY, J. R. 1939. A biological survey of the Lake Ontario watershed. State of New York Supp. to 29th Annu. Rep. XVI: 1–261.

Joliff, T., C. Creech, C. Widemer, and P. C. Neth. 1980 Management of the effects of sea lamprey predation in Seneca and Cayuga lakes. New York State Dep. Environ. Conserv., Albany, New York. 91 p. (Manuscript revised April 15, 1980.)

Jolliff, T. M., and P. C. Neth. 1980. Draft environmental impact statement on experimental sea lamprey reduction in Seneca Lake, New York. New York State Dep. Environ. Conserv., Albany, NY.

Lark, J. G. I. 1973. An early record of the sea lamprey (*Petromyzon marinus*) from Lake Ontario. J. Fish. Res. Board Can. 30: 131–133.

Parsons, J. W. 1973. History of salmon in the Great Lakes, 1850–1970. U.S. Fish Wildl. Serv. Tech. Pap. 68: 80 p.

Pearce, W. A. 1978. Lake Ontario comprehensive fisheries and wildlife management plan (1975). New York State Dep. Environ. Conserv., Cape Vincent, New York 13618. (Under revision)

Shetter, D. S. 1949. A brief history of the sea lamprey problem in Michigan waters. Trans. Am. Fish. Soc. 76(1946): 160–176.

Smith, B. R. 1971. Sea lampreys in the Great Lakes of North America, p. 207–247. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London and New York.

Smith, B. R., and J. J. Tibbles. 1980. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936–78. Can. J. Fish. Aquat. Sci. 37: 1780–1801.

Smith, B. R., J. J. Tibbles, and B. G. H. Johnson. 1974. Control of the sea lamprey (*Petromyzon marinus*) in Lake Superior, 1953–70. Great Lakes Fish. Comm. Tech. Rep. 26: 60 p.

Smith, S. H. 1972. Factors of ecological succession in oligotrophic fish communities of the laurentian Great Lakes. J. Fish. Res. Board Can. 29: 951–957.

Youngs, W. D. 1972. An estimation of lamprey-induced mortality in a lake trout population. Ph.D. thesis, Cornell Univ., Ithaca, NY. 147 p.

Factors Influencing the Distribution of Sea Lamprey (*Petromyzon marinus*) in the Great Lakes[1]

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The sea lamprey (*Petromyzon marinus*) is widely distributed in the Great Lakes but it is absent from or scarce in large parts of the watershed. Since 1957, larval sea lampreys have been detected in only 433 (7.5%) of the 5747 streams in the Great Lakes basin. Parasitic-phase sea lampreys range throughout the lakes, wherever suitable host fishes occur, but probably do not inhabit the western and central basins of Lake Erie to any great extent during summer. Many environmental conditions influence the distribution of sea lampreys. Streamflow and water temperature are of major importance in attracting spawning runs to streams. The dispersal of spawning adults within streams is influenced mainly by blockages, water temperature, current, bottom type, and the presence of inland lakes. Water temperature is probably the most important factor affecting the development and survival of embryos. The distribution of larval lampreys is limited primarily by barriers that block adult spawning runs, warm temperatures, low and unstable flows, hard stream bottom, and pollution; nonetheless, larvae have been found in a wide range of habitats exhibiting these conditions. Interconnecting waterways and attachment to fishes and boats are considered major factors in the lake movements of parasitic-phase lampreys.

Key words: sea lamprey, *Petromyzon marinus*; Great Lakes, geographic distribution, influences, movement, spawning, larvae, parasitic, control

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La grande lamproie marine (*Petromyzon marinus*) est largement répandue dans les Grands Lacs, mais elle est absente ou rare dans de grandes portions du bassin hydrographique. Depuis 1957, on a trouvé des larves de cette lamproie dans seulement 433 (7,5%) des 5747 cours d'eau du bassin des Grands Lacs. Dans sa phase parasitaire, la grande lamproie marine se trouve dans tous les lacs, là où il y a des poissons hôtes convenables. Cependant, elle ne fréquente probablement pas beaucoup les bassins occidental et central du lac Erie én été. Plusieurs facteurs de l'environnement influent sur la distribution de la grande lamproie marine. Le débit et la température de l'eau jouent un rôle important dans le choix des cours d'eau pour la ponte. La dispersion des adultes reproducteurs à l'intérieur des cours d'eau est affectée surtout par les obstructions, température de l'eau, courant, type de fond et présence de lacs intérieurs. La température de l'eau est probablement le facteur le plus important pour le développement et la survie des embryons. La distribution des lamproies larvaires est limitée principalement par les obstacles bloquant les remontées d'adultes reproducteurs, des températures élevées, des débits faibles et instables, un fond dur dans le cours d'eau et la pollution; néanmoins, on a trouvé des larves dans une gamme étendue d'habitats possédant ces caractéristiques. Quant aux déplacements dans les lacs de lamproies dans la phase parasitaire, les voies navigable, ainsi que la fixation à des poissons et à des navires sont considérées comme les principaux agents.

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DISTRIBUTION of sea lamprey (*Petromyzon marinus*) in the Great Lakes watershed (Fig. 1) is determined by the interactions of various physical, chemical, and biological factors. These factors are discussed as they affect the spawning, embryo, larval, and parasitic stages of sea lampreys in stream and lake ecosystems.

This paper is based on the review and analysis of available publications and the unpublished records of the American and Canadian sea lamprey control agents. The unpublished data span almost 30 yr of investigations dealing with each life stage of the animal, and include information from weir operations, stream and lake surveys, lampricide treatments, water quality analysis, and many smaller-scale studies. As the number of ecological factors discussed and the attention given to each were controlled mainly by the available information, this paper will serve to indicate areas where further studies of sea lamprey ecology are needed.

Interconnecting Waterways

Parasitic and prespawning sea lampreys are the most important life stage in expanding the range of this species throughout the Great Lakes because of their habits, mobility, and habitat. The waterways linking together the Great Lakes made possible the invasion and spread of the sea lamprey (Fig. 1). Just how and when the sea lamprey became established in Lake Ontario and in the Finger Lakes of New York are still a matter of conjecture. Fothergill's (undated) description of a spawning male sea lamprey taken from Duffin Creek (Fig. 1), a Lake Ontario tributary, in 1835 is the earliest reliable record available to date from Lake Ontario (Lark 1973). It appears that the sea lamprey was probably established by that time in Lake Ontario and the Finger Lakes (Gage 1893). If so, its migration there may have preceded the completion of the eastern part of the Erie Canal (1823), the first man-made waterway linking the Great Lakes to the Atlantic Ocean (Aron and Smith 1971). Although parasitic-phase sea lampreys are reportedly found in the St. Lawrence River (Scott and Crossman 1973), their origin is unknown. There is no evidence to show any distributional overlap between the marine and Great Lakes forms.

The presence of ammocoete populations in tributaries to the Oswego River (Fig. 1) and the movement of newly transformed and parasitic-phase sea lampreys

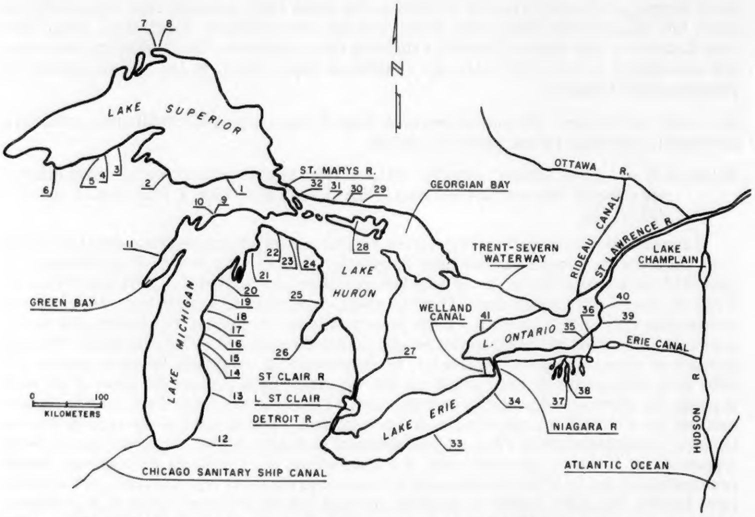
7
8
LAKE SUPERIOR
N
OTTAWA R.
6
5
4
3
2
1
ST. MARYS R.
32
31
30
29
GEORGIAN BAY
10
9
11
28
22
23
24
21
LAKE HURON
TRENT-SEVERN WATERWAY
RIDEAU CANAL
ST LAWRENCE R
LAKE CHAMPLAIN
GREEN BAY
LAKE MICHIGAN
20
19
18
17
16
15
14
13
25
WELLAND CANAL
41
L. ONTARIO
35
36
40
39
ERIE CANAL
26
27
ST CLAIR R
L ST CLAIR
DETROIT R
0
100
KILOMETERS
12
LAKE ERIE
33
34
37
38
NIAGARA R
HUDSON R
ATLANTIC OCEAN
CHICAGO SANITARY SHIP CANAL

FIG. 1. Great Lakes basin, showing major waterways of possible significance in interlake distribution of sea lampreys, and the location (indicated by numbers) of tributary streams mentioned in text: 1, Sucker R. (East Bay); 2, Big Garlic R.; 3, Misery R.; 4, East Sleeping R.; 5, Ontonagon R.; 6, Bad R.; 7, Jackpine R.; 8, Gravel R.; 9, Manistique R.; 10, Bursaw Cr.; 11, Peshtigo R.; 12, St. Joseph R.; 13, Kalamazoo R.; 14, Grand R.; 15, Muskegon R.; 16, White R.; 17, Pere Marquette R.; 18, Manistee R.; 19, Betsie R.; 20, Platte R.; 21, Pine R.; 22, Cheboygan R.; 23, Ocqueoc R.; 24, Schmidt Cr.; 25, Au Sable R.; 26, Saginaw R. (Tittabawassee R.); 27, Bayfield R.; 28, Kagawong R.; 29, Spanish R.; 30, Serpent R.; 31, Blind R.; 32, Thessalon R. (Bridgeland R.); 33, Conneaut Cr.; 34, Cattaraugus Cr.; 35, Blind Sodus Cr.; 36, Oswego R.; 37, Cascadilla Cr.; 38, Falls Cr.; 39, Little Salmon R.; 40, Stony Cr.; and 41, Duffin Cr.

downstream to Lake Ontario from the Oneida–Finger Lakes watershed (Rugen 1977) suggest that interchange takes place between these waters via the central parts of the Erie Barge Canal system (Fig. 1) and the Oswego River. However, the magnitude of this interchange is unknown.

The Welland Canal (Fig. 1), opened originally in 1829, provided the first feasible opportunity for the movement of fishes from Lake Ontario into Lake Erie. Yet it was not until 1921, 92 yr later, that the first sea lamprey was reported above Niagara Falls (Applegate 1950). This extensive time lag suggests that the upstream movement of lampreys through the waterway was minimal. Lamprey movement through the canal would have been thwarted by such conditions as low flow, absence of flow in winter, locks, channel length, and poor water quality. No adult or larval lampreys were found in surveys of the canal in 1959 and 1961 (Dodge 1963). Only one authentic report of a sea lamprey being captured in the canal exists and this specimen probably originated in Lake Erie (Dodge 1963). However, we suspect that the second Welland Canal, built in 1914–32 for handling larger ships (Harris and Levey 1975), may have been easier for sea lampreys to negotiate than the original waterway, thereby facilitating migrations into Lake Erie later than was believed.

A second possible but less likely route used by sea lampreys for migrating between Lake Ontario, the Finger Lakes, and Lake Erie, is the western portion of the Erie Canal, opened in 1825. However, its limitations are similar to but greater than those of the Welland Canal. There could be some movement of lampreys from Lake Erie to Lake Ontario via the Niagara River since the eastern basin of Lake Erie contains nursery streams and a parasitic population.

The Trent–Severn Waterway (Fig. 1), connecting the Bay of Quinte in Lake Ontario to Georgian Bay in Lake Huron, could have provided a possible alternate passageway for sea lampreys to enter the Upper Great Lakes since its completion in 1918. Based on historical evidence, however, the sequence of the invasion proceeded from Lake Erie upward into Lakes Huron and Michigan, then into Lake Superior, suggesting that the Trent–Severn route was not used (Applegate 1950). In addition, its formidable length (386 km), numerous locks (45), and the marine railway on the Georgian Bay end of the waterway would tend to stop migrations.

In a tagging study in the St. Marys River and northern Lakes Huron and Michigan during 1963–67, Moore et al. (1974) found that sea lampreys moved extensively, and interchange between the lakes was common. A total of 2265 lampreys were tagged and released below the navigational locks in the St. Marys River (Fig. 1). Of the 93 recaptured, 80 were taken in Lake Huron, 12 in Lake Superior, and 1 in Lake Erie. In other studies, divers inspecting vessels passing through the Canadian navigation lock in the St. Marys River in 1956 and 1957 found sea lampreys attached to ships only during the fall (Pearson 1957; B. G. H. Johnson 1958). A partial search yielded 13 lampreys on 22 upbound vessels and 3 lampreys on 10 downbound vessels. It is likely that more movement of sea lampreys occurs through the U.S. locks where boat traffic is heavier and lamprey congregations larger. Sea lamprey attachment to vessels moving through the Welland Canal has also been documented (Dodge 1963). Gage (1928) and Creaser (1950) also reported the attachment of sea lampreys to moving objects other than fish. Because commercial cargo traffic has been heavy and widespread in the Great Lakes (Fig. 2), we assume that the attachment of sea lampreys to boat hulls could have been a significant factor in this species' rapid and widespread dispersal.

We do not believe that the Rideau Canal (Fig. 1), linking eastern Lake Ontario to the Ottawa River, was significant in the movement and distribution of sea lampreys because of warm water, shallowness, and the presence of large lakes in some sections of the system. The Chicago Sanitary Ship Canal (Fig. 1), connecting Lake Michigan to the Mississippi River system, was also probably unimportant owing to warm and shallow water, high turbidity, and generally poor water quality.

The extensive movement of parasitic-phase sea lampreys was demonstrated in two tagging studies. In northern Lake Huron in 1951–52, 22 sea lampreys traveled distances up to 336 km in 15 d or more (Smith and Elliott 1953). Moore et al. (1974) recovered 477 of 4048 sea lampreys released in the St. Marys River, northern Lake Huron, and Lake Michigan; and 42 had traveled an average of 275 km (range 160–628 km) before they were recovered.

Physical Barriers

Physical barriers such as waterfalls, cascades, and dams have long been recognized as limiting to the upstream movements of sea lampreys throughout the Great Lakes, Niagara Falls being the classic example. Surface (1899) reported that sea lampreys ascended two tributaries of Cayuga Lake, Cascadilla and Falls creeks (Fig. 1), in large numbers, but waterfalls about 1.6 km above their mouths blocked the migration. The adults left the streams within a week when they were unable to find suitable spawning sites. Even as early as the 1800s, the construction of dams was blamed for the decline of sea lampreys on the east coast of the United States (Goode 1884), and more recently has been shown to be largely responsible for the decline in the European river lamprey (*Lampetra fluviatilis*) fisheries in Finland (Tuunainen et al. 1980). Christie (1973) suggested that the abundance of dams in the 1800s was a reason for the apparently small number of sea lampreys in Lake Ontario during that period. Morman (1979) reported that sea lampreys in the Lower Peninsula of Michigan were excluded from about 60% of the entire drainage network by the presence of dams. Another consideration of dams is

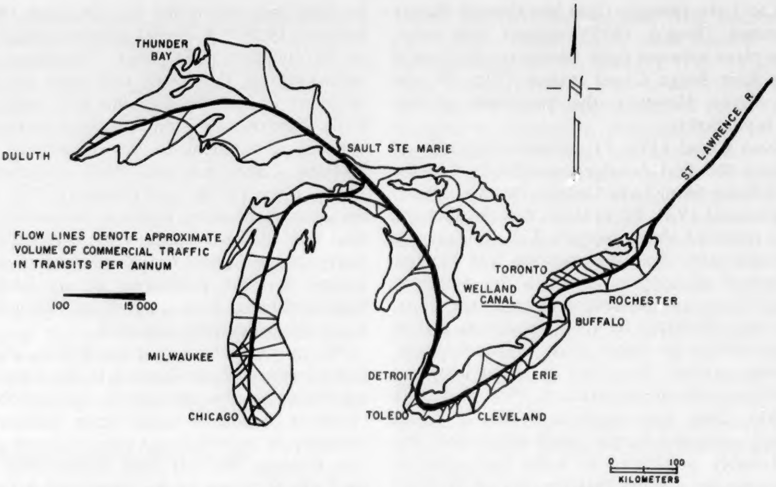

FIG. 2. Routes and volume of commercial cargo traffic in the Great Lakes in 1970. (Adapted from Great Lakes Basin Commission 1976.)

that the survival of larval lampreys downstream from these barriers may be affected by flow manipulation, depleted oxygen levels, and higher water temperatures.

A barrier's influence on lamprey migrations depends largely on its location in the watershed and its blocking capacity during high flows. Applegate and Smith (1951) found that sea lampreys blocked by a dam near the mouth of the Cheboygan River (Fig. 1) returned to Lake Huron and augmented runs in other streams as far as 48 km away. Studies by the U.S. Fish and Wildlife Service indicated that sea lampreys can surmount the dam on the Tittabawassee River (Saginaw River system, Lake Huron) only during floods; a relatively minor cascade falls on the East Sleeping River (Lake Superior) is enough to block adult runs in some years; and on the Little Salmon River (Lake Ontario) sea lamprey adults have migrated upstream past at least three dams of questionable integrity (Fig. 1).

Beaver dams are generally more common on smaller streams or headwater tributaries of larger rivers where their influence on lamprey runs is relatively unimportant. These structures are temporary, pervious, and insufficiently high during spring freshets to block lamprey movements. Sand and gravel bars which form across stream mouths, although transitory, may completely seal off the streams to spawning runs. These bars may exist for periods of a few days to several weeks, and are most common on smaller streams with extensive estuarine areas. Such bars form regularly on several streams along the western shore of Lake Superior for short periods in the summer. Along the Minnesota coast this condition lasts for much longer periods in numerous small streams.

A lamprey's capacity to migrate above barriers is influenced by the physical characteristics of the obstacle, the lamprey's size, degree of sexual maturity, and general physical condition as well as water temperature and velocity, and distance of the barrier above the lake. The minimum criteria presently accepted for a sea lamprey barrier dam are a 45-cm head during lamprey spawning runs with a 15- to 30-cm overhanging lip (Hunn and Youngs 1980). Since the endurance of sea lampreys declines with distance traveled, obstacles that might only momentarily delay runs in the downstream reaches early in the season may stop lampreys farther upstream later on. In the Ocqueoc River (Fig. 1), a tributary of Lake Huron, Applegate (1950) noted that nearly one-half of the spawning migrants surmounted two natural falls, 1.4 and 1.8 m high, and an old mill dam ~15 km from the mouth. On the East Branch of the Ontonagon River (Fig. 1), a tributary of Lake Superior, personnel from the U.S. Fish and Wildlife Service observed that adults were stopped by a dilapidated log dam 90 km upstream from Lake Superior.

Weirs operated on many Great Lakes streams to control sea lampreys reduced both spawning and larval populations in streams and limited upstream distribution in some. Weirs reduced upstream limits of distribution from 20 to 2 km in the Misery River in 1962–70 and since 1953, from 65 to 30 km in the Sucker River, two Lake Superior tributaries (Fig. 1). Recent cessation of weir operations is expected to be followed by an increase in distribution in some Lake Superior tributaries.

Lakes, ponds, and impoundments occur on many streams and probably affect the spawning migration of adult lampreys by modifying stream temperatures and flows, and even increasing the vulnerability of lampreys to predation by fishes. Inland lakes can delay or even reverse the upstream movement of lampreys as suggested by studies conducted by Applegate (1950) on Ocqueoc Lake. Lakes situated at or near the mouths of streams are especially common along the eastern shore of Lake Michigan. Reversing currents up to 1.3 m/s occur in the entrances to even the larger rivers (U.S. Department of Commerce 1974) such as the Pere Marquette, White, Muskegon, and Pine (Fig. 1) and may interfere with detection of stream currents by lampreys or disorient lampreys entering the stream.

Streamflow

It is remarkable that of the 5747 streams in the Great Lakes watershed, only 433 (7.5%) have supported populations of sea lamprey larvae since 1957: 364 in the three upper lakes (Smith and Tibbles 1980) and 69 in the two lower lakes (Pearce et al. 1980). Streams attracting sea lamprey runs are distributed throughout the five lake basins, but are most abundant along the south shore of Lake Superior, the northern halves of Lakes Michigan and Huron, and the eastern half of Lake Ontario. Conversely, spawning runs are absent or rare in tributaries of Lake Erie, the western half of Lake Ontario's south shore, the west shore of Lake Michigan south of Green Bay, and the Minnesota and central Canadian coasts of Lake Superior. Although there is no evidence that sea lampreys "home" to parent streams as do salmonids, their selection is influenced by the interaction of various physical factors, streamflow being a major one.

Streamflow characteristics determine the spawning areas of sea lampreys. Unidirectional water current is considered by most investigators to be an essential requirement for successful spawning. Although Skidmore (1959) documented successful spawning and larval production from nests in still-water areas of the Bridgeland River (Fig. 1), a tributary of the Thessalon River which discharges into Lake Huron, his observations were of animals confined to an enclosure and may not be indicative of any natural behavior. Current velocities at nesting sites on the Ocqueoc River ranged from 0.4 to 1.6 m/s, but were 1.1–1.3 m/s on four heavily used riffles (Applegate 1950).

The largest streams in an area have been observed to attract and accommodate the largest runs if other environmental factors are favorable. Sea lampreys in Quebec were reported to favor the larger volume streams (Vladykov 1952). Presumably, flow from large rivers is more readily detected by lampreys in offshore areas than that from smaller streams (Applegate 1950). Stauffer and Hansen (1958) reported that sea lamprey ammocoete abundance was greater in Lake Superior tributaries with flows larger than 0.8 m^3/s than in those with flows less than 0.3 m^3/s. Nonetheless, sea lamprey larvae inhabit streams ranging widely in size, from small coastal tributaries with flows less than 0.03 m^3/s to large interlake channels, such as the St. Clair River (Fig. 1) with low flows as large as 4400 m^3/s (Morman 1979). The median low flow of 74 streams that contained populations of sea lamprey ammocoetes in the Lower Peninsula of Michigan was 0.4 m^3/s (Morman 1979). In contrast, among 380 streams that did not contain ammocoetes in this region and northern Indiana, 296 (78%) were intermittent or extremely low in flow during late summer (U.S. Fish and Wildlife Service, Ludington, Michigan, unpublished records). We believe that small streams and tributaries of streams are used to a lesser extent by sea lampreys than larger ones because their flows are harder for spawning runs to detect, their mouths are more indistinct and subject to blockages, and many are too cold for spawning or larval production — their main water source is cold springs and groundwater.

Given water, soft substrate for burrowing, tolerable water temperatures, and sufficient oxygen concentrations, ammocoetes seem able to survive in habitats with little, intermittent, or no flow, such as side channels, backwaters, oxbows, pools of intermittent streams, fish ponds, beaver impoundments, and lakes — based on observations made by the authors. The occurrence of larval sea lampreys in the Great Lakes themselves or tributary inland lakes has been well documented (Applegate 1950, 1961; Thomas 1960, 1962, 1963; Great Lakes Fishery Commission 1961–76; Wagner and Stauffer 1962a, b; Hansen and Hayne 1962; Gaylord and Smith 1966; Manion 1969; Smith 1971; Hodges 1972; Morman 1979). Populations of sea lamprey ammocoetes, some containing metamorphosing lampreys, were detected in isolated pools of 10 intermittent tributaries to northern Lake Huron, in the Lower Peninsula of Michigan, in the summer of 1966 (U.S. Fish and Wildlife Service, Ludington, Michigan, unpublished records). Larvae were collected from eight of these streams in the following spring. Ammocoetes have been collected with electroshockers by a survey crew of the U.S. Fish and Wildlife Service from stream banks, 0.9–1.2 m above the water's edge, in the Muskegon River, several hours after water flows were reduced by partial closure of a hydroelectric dam. However, in the same stream, larvae stranded on sand–silt bars were found dead. Possibly spring seepages in the banks may have allowed ammocoetes to survive there.

On the other hand, there are cases where flow intermittency has been limiting to ammocoete populations. H. Purvis (U.S. Fish and Wildlife Service, Marquette, Michigan, personal communication) attributed the loss of two year-classes of sea lamprey larvae in Bursaw Creek (Fig. 1), a northern Lake Michigan tributary, to intermittent flow. The ammocoetes survived part of the summer highly concentrated in pools, but disappeared by fall possibly because of overcrowding, high water temperatures, and low oxygen. Low flow conditions were cited as the probable cause for the disappearance of other lamprey species from streams (Trautman 1957; Bailey 1959; Scott and Crossman 1973). Low and unstable flows were mentioned as two of the major limiting factors — along with pollution, sedimentation, and hard or unstable bottoms — for the absence or scarcity of larvae in streams in the southern half of the Lower Peninsula of Michigan (Morman 1979). There, especially in drainages along the eastern coast of the Peninsula which lie on impervious, clayey lake bed plains (Veatch 1953) and are therefore exposed to frequent and large runoffs, much of the soft bottom material used for ammocoete burrows is flushed into the lakes. Bottoms in these drainages are mainly rubble, gravel, and hardpan clay according to surveys by the U.S. Fish and Wildlife Service. High water velocities and the associated scarcity of soft substrate in short, high-gradient tributaries of Lake Superior have caused larval populations to either leave the stream or die off after 1 or 2 yr (Smith and Braem 1975).

Relatively large populations of sea lamprey larvae inhabit sections of streams, such as in two Lake Michigan tributaries, the Manistee and Muskegon rivers (Fig. 1), where daily water flows and levels, controlled by hydroelectric plants, fluctuate drastically. In conducting surveys on these streams, R. Morman has observed that larvae are discretely distributed, being restricted mainly to habitats stabilized by obstructions and aquatic vegetation and those least susceptible to scouring. For the most part, larvae seem to adjust to the flow pattern, inhabiting bottoms that remain below the water surface during periods of low flow. Flooding has a major impact on lamprey larvae, usually by disturbing the stream substrate, and as Potter (1970) emphasized, is undoubtedly a primary factor in the redistribution of larvae within a stream system. This viewpoint is contrary to Baxter's (1957) belief that larval beds remain undisturbed under all levels of flow except when floods follow drought conditions.

Current velocity largely influences the deposition of substrate particles and the accumulation of organic material (Hynes 1970). Thus, where water velocity is low, soft substrates will form providing suitable habitats for ammocoetes. In contradiction to Schroll's (1959) findings that velocities over larval burrows were 0.6 m/s, Thomas (1962) reported that, since soft bottom can only form in slow currents, ammocoetes were concentrated in the low-velocity parts of a stream's high-velocity sections (mean velocity 0.2–0.3 m/s), but were evenly distributed throughout the entire streambed in a low-velocity section (mean velocity <0.2 m/s).

Water currents play an important role in carrying the newly transformed lampreys into the lakes from the parental stream and in dispersing the lampreys within the lakes. Increasing stream volumes are believed to be of primary importance in triggering the downstream movement of newly transformed sea lampreys (Applegate and Brynildson 1952; Applegate 1961; Hodges 1972; Manion and Smith 1978). However, it is not known if, in the absence of increasing flow, transformed lampreys would remain in the stream for prolonged periods of time until flows increased.

Spawning runs as well as ammocoete populations have occurred in streams ranging in length from 2 km to several hundred kilometres. Despite their poor swimming performance in comparison with most teleosts (Beamish 1974), sea lampreys migrate long distances within streams as shown by the upper limits of ammocoete distribution. Upstream limits of larval sea lampreys in the Saginaw River (Lake Huron) and Grand River (Lake Michigan; Fig. 1) are 181 km and 168 km above their mouths, respectively, despite degraded water quality in the main streams (Morman 1979). Runs in the longest streams in the Great Lakes watershed are usually blocked or hampered by physical barriers and otherwise unfavorable conditions such as pollution.

Water Temperature

Parasitic-phase sea lampreys seem to prefer the hypolimnetic waters of the Great Lakes in spring during the early part of their parasitic life and warmer (6–15°C), shallower water during summer (Applegate 1950). However, in the absence of suitable host fish in deep water, lampreys will live in relatively warm water as they did in Lake Ontario for many years prior to the introduction of salmonids in the late 1960s (Christie 1973; Christie and Kolenosky 1980). G. J. Farmer and F. W. H. Beamish (Great Lakes Fish. Comm., June 1973, mimeograph) and Farmer et al. (1977) demonstrated that adult sea lampreys survived and grew in water temperatures of 4–20°C.

With hypolimnetic temperatures near a constant 4°C and surface temperatures reaching an average summer maximum of about 13°C for Lake Superior, 20°C for Lakes Michigan and Huron, and 22°C for Lake Ontario (Miller 1952), temperature alone should not limit the distribution of sea lampreys in these deepest Great Lakes.

Applegate (1950) observed that the timing, consistency, and duration of spawning runs were closely related to temperature in streams and adjacent areas of the lake. The validity of these observations was reinforced by other investigators (Wigley 1959; Skidmore 1959; Manion and McLain 1971) and records from numerous lamprey control weirs operated by the U.S. Fish and Wildlife Service on the Upper Great Lakes for about 30 yr.

Sea lampreys have been observed to begin their upstream migration when stream temperatures reach 3–4°C and also exceed the temperature of the adjacent lake by several degrees (Applegate 1950). The peak migration coincides with temperatures that remain above 10°C. Migration continues at a relatively high level until temperatures exceed 18°C. Occasional stragglers may enter streams and spawn as late as September (Morman 1979). Runs are erratic and of shorter duration in small runoff streams where water temperatures may be quite unstable. Conversely, runs are steadier and last longer in stable flowing streams. Water temperatures ~11–25°C appear essential for successful spawning, although P. Rugen has observed spawning in the Bad River (Fig. 1), a Lake Superior tributary, with a midday temperature of 27.8°C in late June. He did not determine if this spawning was successful. When streams do not warm up rapidly enough they may be abandoned by lampreys which then return to the lake to seek more suitable streams (Applegate 1950). Low water temperatures were cited by stream survey personnel of the U.S. Fish and Wildlife Service as the apparent reason for the absence of sea lampreys in numerous streams on Lake Superior. A. H. Lawrie (AAAS Meeting, Chicago, December 1970, unpublished data) suggested that the relatively cool summer climate along the central portion of Lake Superior's north shore depresses stream temperatures, resulting in sparse use by spawning lampreys. Smith (1978) believed that the sea lamprey was reaching the northern extreme of its range in the Great Lakes basin.

Certainly the distribution of spawning lampreys within a stream is influenced by variations in water temperature patterns between segments of the system. The restriction of larval lampreys to only certain segments of most drainages and their absence from warm-water and extremely cold-water habitats tend to indicate either that spawning lampreys avoid some areas or that their larvae fail to survive in areas exposed to temperature extremes. Morman (1979) noted the exclusion of sea lampreys from low temperature habitats unoccupied by lamprey larvae altogether or occupied exclusively by American brook lampreys (*Lampetra lamottei*); and from high temperature habitats where *Ichthyomyzon* species, particularly *I. fossor*, were present. Stauffer and Hansen (1958) reported that sea lamprey larvae rarely occurred in cool, spring-fed streams where slimy sculpins (*Cottus cognatus*) and brook trout (*Salvelinus fontinalis*) were abundant. In fact, these habitats may have been too cold for sea lamprey production, like those Morman (1979) noted; or they were not used merely because of the low density of spawning run adults during this early period in the history of the sea lamprey in Lake Superior.

Among environmental factors influencing the development of sea lamprey embryos, water temperature is perhaps the most important. Using fluctuating temperatures, Piavis (1971) reared sea lamprey embryos most successfully in the ranges 18.4–23.9°C and 15.5–21.1°C. Later studies demonstrated that embryos could develop at much lower temperatures (10.0–11.7°C), although development was slow (Manion and Hanson 1980). Applegate (1950) reported a mean daily temperature range of 18.6–24.2°C with daily extremes of 16.1–26.1°C in the Ocqueoc River during development and hatching of sea lamprey embryos.

Sea lamprey ammocoetes are incapable of surviving at water temperatures much higher than 30°C (McCauley 1963; Potter and Beamish 1975; Macey and Potter 1978), although burrowed larvae can survive lethal temperatures for a longer period than unburrowed larvae (Potter and Beamish 1975). The maximum water temperatures recorded during 1958–77 surveys in the United States, in habitats containing sea lamprey larvae, ranged from 21.7 to 31.1°C among 101 Great Lakes tributaries (U.S. Fish and Wildlife Service, unpublished records). Stauffer and Hansen (1958) reported that ammocoetes were most abundant in streams with summer temperatures of 10–26.1°C, and were rare at temperatures outside this range. Average temperatures of 15–20°C in June-August were recorded in 13 Lake Superior tributaries supporting sea lamprey larvae (Manion and McLain 1971). The experimental temperature preferendum of sea lamprey larvae ranged from 10 to 19°C with a mean of 13.6°C (Reynolds and Casterlin 1978). D. Cuddy believes the absence of ammocoetes during late summer from the lower sections of Lake Ontario streams, the upper sections of which support lampreys, may be due to high water temperatures. Also, he observed in a number of streams characterized by high summer temperatures, such as Blind Sodus Creek (Lake Ontario) and the Bayfield River (Lake Huron; Fig. 1), that the distribution of lamprey larvae was limited to areas of groundwater inflow. However, Applegate (1950) noted that in cooler streams, ammocoetes avoided habitats influenced by cold springs and seepages.

Streambed

Sea lampreys require mostly gravel (15–115 mm diameter) for constructing nests, although they use other materials such as rubble, clam shells, and lumps of clay when gravel is scarce or absent. In streams void of gravel, the incidental introduction of gravel at highway and railroad crossings provides lampreys with spawning sites. In such streams spawning may be limited to only one small area. Thomas (1962) noted that one of the major factors controlling ammocoete distribution is the location of spawning sites. Observations by R. Morman indicated that the distribution of larvae in the large producing streams in the Lower Peninsula of Michigan, for example, was closely associated with the spawning areas. Generally, larval density is inversely related to the distance downstream from spawning areas, although, as Morman (1979) suggested, habitats in the lower reaches of these streams may be unsuitable for sea lamprey ammocoetes. Surveys conducted by the U.S. Fish and Wildlife Service showed that the absence of suitable spawning habitat was a limiting factor in 118 of 380 streams in the Lower Peninsula that did not support populations of sea lamprey larvae.

The larvae of sea lamprey occur most frequently in soft bottoms containing mixtures mainly of silt and sand (Applegate 1950; Wilson 1955; Stauffer and Hansen 1958; Wigley 1959; Manion and McLain 1971; Manion and Smith 1978). The more favorable habitats probably contain clay-size particles as well (Hardisty and Potter 1971a). However, both Thomas (1962) and Morman (1979) referred to the scarcity of ammocoetes in the lower sections of some streams in spite of soft bottoms, suggesting that heavy siltation and slow currents were unfavorable. Presumably, lampreys were excluded from streams in the glaciated portions of the State of Illinois mainly because of silt and turbidity (Starrett et al. 1960). Partially supporting this viewpoint, Leach (1946) observed in laboratory studies that ammocoetes developed respiratory problems in muddy waters. A study of the preference of sea lamprey larvae (70–120 mm long) for various bottom materials demonstrated that 89.9% of the larvae selected sand over gravel, 77% chose sand over silt, and none selected clay over sand (Erkkila 1962). Applegate (1950) and Morman (1979) noted that sea lamprey ammocoetes avoided unstable, sandy bottoms. D. Cuddy suspects that most ammocoetes produced in the Gravel River (Fig. 1), a tributary of Lake Superior, migrate to lentic habitats off the mouth because of the unstable, sandy bottom. Personnel from the Department of Fisheries and Oceans of Canada attributed the absence of stream populations in the Kagawong (Lake Huron) and Jackpine (Lake Superior) rivers (Fig. 1) but the presence of populations off their mouths to the lack of soft substrates in the streams. Furthermore, their observations indicated that sea lamprey ammocoetes were confined to the banks of the Spanish River (Lake Huron; Fig. 1) and seemed to avoid the bottom in midstream, which is covered with wood fiber mats produced by a paper pulp industry. Some lamprey larvae can be found in almost every habitat (Applegate 1950; Manion and McLain 1971; Manion and Smith 1978), even "in the interstices of stones, in gravel, under wood, old tires, and other debris and in very small pockets of soft sediment among rocks" (Thomas 1962). Applegate (1950) observed that the largest concentrations of ammocoetes in a given bed were among small patches of aquatic plants, predominantly *Najas flexilis, Potamogeton epihydrus*, and species of *Sagittaria*.

The effects of anchor ice on the distribution of larval lampreys has not been investigated. Manion and McLain (1971) mentioned it as a possible causal factor in the mortality of larvae in the Big Garlic River (Fig. 1), a Lake Superior tributary.

Chemical Factors and Pollution

Beamish (1973) reported that the oxygen consumption of adult sea lampreys at various temperatures was comparable to salmonids of similar weight. Except for Lake Erie and some localized areas, the Great Lakes have adequate oxygen levels throughout the year (Beeton 1969). In Lake Erie, the hypolimnion of the central basin experiences severe oxygen depletion during summer (Beeton 1963). Surveys in late summer in 1959 and 1960 showed dissolved oxygen concentrations <3 mg/L in about 75% of the central basin (Beeton 1963). During stratification, only the hypolimnion in the eastern basin maintains oxygen levels adequate to support fishes with high oxygen needs.

Low oxygen alone can rarely be considered a major factor limiting the distribution of sea lamprey larvae, for two reasons. First, ammocoetes can tolerate low oxygen levels because of low metabolic activity (Randall 1972) and their blood characteristics and branchial pumping ability (Potter et al. 1970). Potter and Rogers (1972) demonstrated that unburrowed ammocoetes consumed oxygen at a higher rate ($245\ \mu L \cdot g^{-1} \cdot h^{-1}$) than burrowed ammocoetes ($110\ \mu L \cdot g^{-1} \cdot h^{-1}$) under otherwise similar conditions. The average oxygen consumption of large unburrowed sea lamprey larvae (mean 120–148 mm) was 0.159–0.217 $mg \cdot g^{-1} \cdot h^{-1}$ at 18°C and 0.414–0.643 $mg \cdot g^{-1} \cdot h^{-1}$ at 22.5°C (Leach 1946), although such comparatively high values may have been due to the absence of a substrate and an insufficient resting period (Potter et al. 1970; Lewis 1980). Sea lamprey ammocoetes were collected by the U.S. Fish and Wildlife Service in July 1962 from a still-water pool in an intermittent Lake Huron tributary, Schmidt Creek (Fig. 1), where the oxygen concentration was 2.3 mg/L and the temperature was 15.6°C, although their occurrence in such habitats was atypical. However, there are other cases where low oxygen apparently limited the distribution of larval lampreys (Smith and King 1970; Morman 1979; Kainua and Valtonen 1980; Tuunainen et al. 1980; Valtonen 1980). Second, more harmful conditions such as pollution and high water temperatures usually occur in association with low oxygen levels.

The influence of stream pollution on spawning runs of sea lampreys is poorly understood. Adult lampreys may be more tolerant of some pollutants than embryonic or larval lampreys since they run polluted streams in which larvae have never been detected. Sea lampreys migrate through heavily polluted main streams of rivers such as the Grand, Kalamazoo, St. Joseph, and Saginaw in the Lower Peninsula of Michigan (Fig. 1) and spawn successfully in their relatively clean tributaries, as determined in surveys conducted by the U.S. Fish and Wildlife Service. Sea lampreys were observed spawning in a heavily polluted section of the Tittabawassee River (Saginaw system) in Midland, Michigan, in May 1979, and presumably spawned there in other years, yet larvae have never been collected there. As a consequence of pollution abatement, our surveys have shown that larval lampreys have become established in the Peshtigo River on Lake Michigan and increased in numbers in Cattaraugus and Conneaut creeks on Lake Erie (Fig. 1).

Various types of pollution, either alone or in combination with other adverse conditions, limit the distribution of sea lampreys. Mortality, delayed hatching, and deviations from normal development of sea lamprey embryos were induced in laboratory experiments by exposure to various chemical agents (Piavis 1962, 1971; Piavis and Howell 1975). Streams in the southern half of Michigan's Lower Peninsula where pollution from urbanization, agriculture, and industry are commonplace contain small, discrete larval sea lamprey populations. Streams in the less-developed northern half, where water quality is comparatively high, support large, widely distributed populations (Morman 1979). Stream pollution has also been cited as a limiting factor in the Lake Erie drainage (Trautman 1949, 1957; Lawrie 1970; Leach and Nepszy 1976) and in streams entering the western half of Lake Ontario along the southern shore (T. Jolliff, New York State Department of Environmental Conservation, Cape Vincent, New York, personal communication). Sluggish flow and warm water are probable factors in the latter basin (Christie and Kolenosky 1980). All but 1 of the 25 Lake Ontario tributaries in the United States that support sea lamprey populations occur in the southeastern drainage where agriculture and industrialization are less intense. In spite of the limiting effects of pollution on lamprey distribution, most ammocoetes found during lampricide treatment of the Blind River (Fig. 1), a tributary of Lake Huron, in 1971, were in a lagoon heavily contaminated with raw untreated municipal sewage.

In Stony Creek (Fig. 1), a tributary to the eastern shore of Lake Ontario, a larval population died off in the summer of 1974. D. Cuddy considered the cause to be pollution in combination with high water temperatures. Differences in survival rates of ammocoetes between polluted streams might be explained on the basis of the stream volume–sewage volume ratio, comparative levels of critical chemical constituents, and water temperatures, although this problem has not been studied. Pollution of streams was considered a major cause of decimation for other lamprey species in the United States (Trautman 1957; Starrett et al. 1960) and in Europe (Schroll 1959; Hardisty 1961; Sterba 1962; Maitland 1980; Tuunainen et al. 1980). Contaminants, although greatly diluted in stream water, may reach toxic levels as they accumulate in the sediments and thereby cause mortality of larval lampreys (Sterba 1962). Also, the ingestion of contaminated food organisms could have deleterious effects on larvae. However, no ammocoetes have been tested for contaminant levels.

Thomas (1962) failed to show any correlation between conductivity, or pH, and sea lamprey abundance. Personnel from the Canadian and U.S. sea lamprey control units have found larvae in streams with slightly acidic waters (pH 6) and even small numbers in the Serpent River (Fig. 1), a tributary of Lake Huron, where pH values have been recorded as low as 5.6. Sterba (1962) states that in central European streams, larval lamprey populations (species unknown) are almost always associated with slightly acid waters.

Formation of marsh gas (CH_4) in bottom habitats was considered to be the reason for the mortality and disappearance of sea lamprey larvae from areas where they were formerly abundant (Wilson 1955).

Ammocoete Movement

Large numbers of sea lamprey larvae move downstream in some rivers (Applegate and Brynildson 1952; Applegate 1961; Manion and McLain 1971; Manion and Smith 1978). Such movements may be common and widespread and are demonstrated by the occurrence of ammocoetes in lentic habitats off the mouths of many streams in the Upper Great Lakes. Lentic populations of sea lamprey ammocoetes have been estimated as large as 52 000 in Batchawana Bay (Thomas 1962) and 96 000 in East Bay (Wagner and Stauffer 1962a) in Lake Superior. Morman (1979) believes, however, that the major translocation of ammocoetes from upper to lower reaches, which Hardisty and Potter (1971a) considered a common phenomenon, does not seem to occur in four of the streams he studied because the different species (*Ichthyomyzon*, American brook, and sea lampreys) were largely segregated along the stream course into gross ecological zones. In streams in which American brook and sea lampreys predominated in the upper zones, these species were comparatively sparse in the lower zones where *Ichthyomyzon* was dominant. It appears that ammocoete movement therefore differs between streams owing probably to variations in such conditions as flow and bottom stability, current velocity, flooding, and ammocoete density in relation to preferred habitat.

Baxter (1957) and Hardisty and Potter (1971a) suggested that in some streams, particularly those with low gradients, stable flows, and suitable habitats, the downstream migration of lamprey larvae is minimal. Manion and McLain (1971), using marked sea lamprey ammocoetes, concluded that a large proportion of the population was static. In spite of densities as high as 170/m^2, western brook lamprey (*Lampetra richardsoni*) larvae apparently moved very little (Scott and Crossman 1973). It appeared to Leach (1940) that ammocoetes moved only when the substrate was disturbed or when food was in short supply. Fogelin (1972, cited by Sjoberg 1980) suggested that downstream movements in Swedish rivers may be a mechanism for self-regulating population size, since the "surplus" of ammocoetes will die after migrating into seawater, of which they are intolerant (Morris 1980). Since sea lamprey larvae could survive migration into the Great Lakes, these lentic populations may have been a major source of recruitment to the parasitic population especially during the period of control by lampricide treatment of streams (1958–79). We believe that the origin of parasitic-phase sea lampreys in the Upper Great Lakes in recent years is ammocoete populations in lentic environments and untreated streams, such as the St. Marys and St. Clair rivers (Fig. 1), and those surviving stream treatments.

Although most migration is downstream, some minimal upstream movement has been reported (Smith and McLain 1962; Thomas 1962; Tibbles 1967; Manion 1969; Smith and King 1970). The upstream movement noted by Thomas (1962) and Tibbles (1967) was from lakes to streams. Observations by the U.S. Fish and Wildlife Service showed that impoundments and inland lakes on streams in the Lower Peninsula of Michigan appeared to prevent ammocoete movement to downstream sections. Although areas above impoundments on the Manistee River of Lake Michigan and the Au Sable River of Lake Huron (Fig. 1), for example, supported high larval lamprey densities, migration to downstream areas was negligible or nonexistent. Once the Homestead impoundment on the Betsie River (Fig. 1), a tributary of Lake Michigan, was permanently drained, American brook lamprey larvae migrated downstream in large numbers. Moreover, sea lamprey larvae have not been detected off the mouths of Lake Michigan tributaries with base-level lakes at their mouths, such as the Platte, Manistee, and Pere Marquette rivers (Fig. 1), based on surveys conducted with an electric trawl and lampricide by the U.S. Fish and Wildlife Service.

Food

The spatial distribution of host fishes in the lakes varies considerably among species and according to season. Generally most waters up to 180 m or more in depth in Lakes Huron, Michigan, and Superior are used by at least one potential host species (Dryer 1966; Lawrie and Rahrer 1973). Johnson and Anderson (1980) reported that their collections of sea lampreys from the commercial fishery in the Great Lakes indicate that there are no limits to the depth distribution of this species; sea lampreys may be found wherever host fishes occur. Since the late 1960s the introduction and continued stocking of salmonids in Lake Ontario and to a lesser extent in Lake Erie have repopulated the previously depleted deeper and offshore waters (Christie 1973; Hartman 1973) and presumably broadened the distribution of lampreys.

Whitefish (*Coregonus clupeaformis*), lake herring (*C. artedii*), lake trout (*Salvelinus namaycush*), and burbot (*Lota lota*) change their vertical distribution seasonally and may therefore influence the vertical distribution of lampreys. Pycha and King (1975) provided evidence that newly transformed sea lampreys may be transported by fish from the general area of the parent stream farther into the lake; during peak lamprey abundance in Lake Superior in the late 1950s commercial fishermen found "hundreds" of lampreys attached to lake herring during herring spawning runs in late November–early December. Although laboratory feeding studies have shown that the sea lamprey has host preferences (G. J. Farmer and F. W. H. Beamish mimeograph), it will apparently attack and feed upon almost any available fish in the absence of "preferred" prey (Smith 1968).

Food of larval lampreys includes a wide variety of organisms, although algae, particularly diatoms, are considered the most important (Creaser and Hann 1929; Schroll 1959; Wigley 1959; Battle and Hayashida 1965; Manion 1967; Manion and McLain 1971; Moore 1972; Moore and Beamish 1973). The distribution and abundance of food organisms may be positively correlated with that of larval lampreys, although Moore (1980), using planktonic bacteria, was unable to demonstrate this association in laboratory experiments. Plankton increase downstream (Hynes 1970), but may be more abundant in the middle than in the lower sections (Blum 1956) of a stream. This distribution corresponds with that of larval sea lampreys in most streams in the Lower Peninsula of Michigan, based on observations by R. Morman. Schroll (1959) reported that ammocoetes were more abundant in streams with high densities of diatoms.

Competition

Competition between sea lamprey and the other two parasitic lampreys, the chestnut lamprey (*Ichthyomyzon castaneus*) and the silver lamprey (*I. unicuspis*), found in the Great Lakes has probably not limited the distribution and abundance of the sea lamprey. Hubbs and Trautman (1937) considered competition a plausible explanation for the absence of silver lamprey from the Lake Ontario drainage where it was replaced by the sea lamprey, and for the absence of chestnut lamprey from the Lake Huron drainage where it was absorbed, through hybridization, by the more dominant silver lamprey. Moreover, they wondered if the sea lamprey, because of its recent invasion of the Upper Great Lakes, would partially or wholly replace *Ichthyomyzon* spp. The silver lamprey has been recorded from all lakes, but is now generally uncommon (Trautman 1957; Morman 1979; Schuldt and Goold 1980). The chestnut lamprey which occurs only in the Lake Michigan basin is mainly an inhabitant of rivers, thus it rarely overlaps with parasitic sea lampreys. When spawning, however, the sea lamprey commonly shares nests with other lamprey species (Morman 1979). Numbers of chestnut and silver lampreys presumably are kept in check by natural controls, although such man-related factors as dams, pollution (Morman 1979), and lampricide treatment of streams (Schuldt and Goold 1980) are contributory.

Competition between parasitic-phase sea lampreys does not seem to have limited their distribution to any extent in the Great Lakes. We assume that the dispersal and ultimate distribution of lampreys entering the lakes from their parent streams would depend somewhat on the numbers migrating from the streams. Therefore, high densities of parasitic-phase lampreys in the Great Lakes may be geographically associated with highly productive nursery streams. Although specific studies on the lampreys are lacking, the direct relationship between population density and extent of dispersal has been shown with other fish populations. W. E. Johnson (1958) found that in years when large numbers of sockeye salmon fry (*Oncorhynchus nerka*) entered Babine Lake, British Columbia, they dispersed farther than in years when small numbers migrated.

The progressive invasion of the sea lamprey into the Upper Great Lakes suggests a population density effect. Lake Superior remained essentially free of lampreys until Lakes Huron and Michigan had large populations. Within Lake Superior, the relatively isolated Superior

Shoal lake trout population did not suffer from lamprey predation until the shore population of lampreys increased (Budd 1954). Competition for host fishes may have influenced the early dispersal of lampreys. As preferred host fish populations were decimated, lampreys probably migrated in search of food. However, there is insufficient evidence to indicate reliably whether the spread of the sea lamprey was essentially passive and random, for example, by attachment to fish and boats, or active and directed such as in searching for prey.

There is no direct evidence that interspecific competition occurs among larval lampreys. Morman (1979) showed that the larvae of different species of lampreys are broadly segregated within streams, and suggested that it was due to differential selection of habitats rather than competition. Scott and Crossman (1973) thought that sea lamprey ammocoetes may compete with other species of ammocoetes for food and habitat, although studies by Moore (1972) and Moore and Beamish (1973) indicated that the number of algae eaten by ammocoetes, in relation to their abundance in the stream, was insignificant. Larval sea lampreys occur in more streams in the Lower Peninsula of Michigan than do the larvae of the other species of lampreys inhabiting that region (Morman 1979). However, this species' predominance when compared to the *Ichthyomyzon* species, is attributable more to the availability of preferred habitats, dispersive capacity, and life habits than it is to competition.

Predators, Parasites, and Pathogens

Distribution of sea lampreys is probably not influenced to any great extent by predators, parasites, or pathogens. Downstream movement of newly transformed lampreys takes place primarily during the night. Thus, predation by diurnal birds and mammals is minimal. Furthermore, since these movements are correlated with increased water flow, the migrants would be provided additional "cover" by the associated increase in water depth and turbidity.

Surface (1899) noted predation on spawning adults by raccoons, muskrats, rats, weasels, foxes, hawks, owls, herons, bitterns, water snakes, and bowfin (*Amia calva*). Applegate (1950) observed domestic dogs removing lampreys from spawning riffles. He also reported predation by gulls below the tailrace of the paper mill on the Manistique River (Fig. 1), a tributary of Lake Michigan, and considered gulls to be the principal predator on adult lampreys in Michigan. R. Torblaa (U.S. Fish and Wildlife Service, Marquette, Michigan, personal communication) found three adults in the stomach of an 8.2-kg northern pike (*Esox lucius*) caught in the spring in Saux Head Lake on the Big Garlic River. Lampreys on nests are probably most vulnerable to predators because they are more exposed in relatively shallow water and are not cautious. Therefore, in streams with few spawners, predators could prevent successful spawning.

Although hatching success of sea lampreys based on potential egg production was estimated to be 0.4–1.1% (Applegate 1950) and 5.3–7.8% (Manion 1968), the survival of eggs deposited in nests averaged about 90% (Manion and Hanson 1980). Large numbers of eggs are lost from nests and swept downstream where they suffer high mortalities, caused in part by predation (Manion and Hanson 1980). It is assumed that larval lampreys are largely immune from predation because of their burrowing, sedentary habits (Churchill 1947; Pletcher 1963; Hardisty and Potter 1971a; Manion and Smith 1978). However, evidence that ammocoetes are readily eaten by predatory fish is found in their formerly common and widespread use as bait (Gage 1928; Schultz 1930; Vladykov 1949; Pletcher 1963; Scott and Crossman 1973). In fact, the possibility that sea lampreys were introduced into Lake Ontario from the Atlantic drainage, or from Lake Ontario into the Upper Great Lakes drainage, by the transportation and inadvertent release of bait ammocoetes should be considered along with other, more widely known hypotheses concerning dispersal. The range of several native minnows in the Great Lakes watershed was expanded in this manner (Hubbs and Lagler 1974).

Sea lampreys are lightly parasitized (McLain 1952; Wilson and Ronald 1967), thus their distribution is unaffected by parasites.

Water Depth

The vertical distribution of sea lampreys in the Great Lakes does not appear to be limited by depth or pressure. Anadromous sea lampreys, although normally found in comparatively shallow water off the North American coast of the Atlantic Ocean (Hardisty and Potter 1971b), are not infrequently taken at depths of 500 m and have been recorded at 4099 m (Haedrich 1977). The maximum depth in the Great Lakes is 406 m (Lake Superior). Applegate (1950) reported that sea lampreys were commonly captured from Lake Huron at depths ranging from 3 to 165 m. Johnson and Anderson (1980) reported that lampreys were captured coincidentally by commercial fishermen at depths of 2–183 m. The greatest numbers were taken from water 2–39 m deep, but as fishing effort was more intensive there, a depth preference is not implied by the observation. Most lampreys in the early part of their parasitic life, which are caught by commercial and experimental fishing during the winter and spring, occur offshore in relatively deep water, 60–150 m (Applegate 1950; Johnson 1969). Catches indicate a gradual shoreward shift during summer and early fall. By late fall most lampreys that will spawn the following spring are found in the shallow waters of bays, inlets, and river mouths. They apparently remain in shallow water throughout the winter, then proceed on their spawning migrations in the spring.

Water depth does not appear to be a critical factor in the distribution of lamprey spawning. Water depth at spawning grounds in 32 northern Michigan streams ranged from 5 to 152 cm, and the average depth over nests in the Ocqueoc River was 23–51 cm with extremes of 15–81 cm (Applegate 1950). A sea lamprey was found by divers on a nest in Lake Huron near the entrance to the St. Clair River at a depth of about 3.7 m (A. K. Lamsa and R. W. Westman, Annu. Rep. Dep. Environ. to Great Lakes Fish. Comm., 1971-1972, Append. 12, mimeograph). Based on these observations, depth is probably limiting only insofar as it affects water currents, reducing them to unsuitable levels for either spawning or embryonic development.

Ammocoetes inhabit water depths at least up to 2.2 m in streams (Applegate 1950) and 16 m in lakes (Morman 1979). In streams, larger ammocoetes were found more commonly in deep water (Wagner and Stauffer 1962a; Manion and McLain 1971; Manion and Smith 1978). Based on the observations of U.S. Fish and Wildlife Service personnel who conducted lamprey distribution surveys, ammocoetes occurred in areas of the stream wherever the bottom and water current were suitable, regardless of water depth. Similarly, Thomas (1962) was not able to correlate ammocoete abundance with water depth.

Larval Lamprey Populations

Moore and Schleen (1980) suggested that spawning-run sea lampreys are attracted to streams containing ammocoete populations. The number of adults captured at control weirs declines drastically in the 1st yr after the ammocoetes are eliminated by lampricide treatment. However, if the treatments are effected in the spring or early summer before the spawning run is finished, and ammocoetes become reestablished, no such decline is apparent in the next year. Ongoing investigations with chemical attractants show that sexually immature sea lamprey migrants (males) select water containing rinses from ammocoetes over other water (Teeter 1980).

Illumination

Hardisty and Potter (1971a) reviewed field and laboratory studies which showed that larval lampreys are photosensitive and have diurnal activity rhythms. Larvae avoid light so that under normal environmental conditions, they emerge from their burrows and swim only during darkness. However, it is assumed that contact stimulation of the burrow is more important than light intensity in reducing swimming activity. Reynolds and Casterlin (1979) reported that in their photokinetic experiments with sea lamprey larvae, mean hourly activity was slightly greater during the day than at night with the peak hourly activity occurring during the dawn crepuscular period as light levels were increasing. Our observations support those reported by Thomas (1962), who found no significant correlation between larval sea lamprey density and illumination.

General Discussion

Numerous factors affect the distribution of the sea lamprey in the Great Lakes drainage. Interconnecting waterways were essential for its original invasion and spread. The geographic location of nursery streams and the distribution of host fish populations are probably the two most important factors influencing the distribution of parasitic-phase sea lampreys. Lampreys produced in streams tributary to regions of the lakes where fishes are concentrated would not have to travel far to find prey, although the high mobility of sea lampreys (Moore et al. 1974) would enable them to travel great distances in search of hosts. Passive movement, by attachment to fish and boats, is also apparently significant in the dispersal of parasitic-phase sea lampreys. Therefore, the role of introduced migratory salmonids as a dispersal agent for sea lampreys in the Great Lakes may be a potentially important consideration in the development of future control strategies. More work is needed on the dispersal patterns of sea lampreys from the natal stream. Filling this gap in the biology of the sea lamprey could lead to new, more acceptable control schemes.

Physical barriers on streams, streamflow, water temperature, and streambed have the profoundest influence on the distribution of spawning sea lampreys. But more knowledge is needed of factors that affect their behavior — particularly what attracts them to one stream in preference to another of apparent similar quality, whether the attraction differs between the sexes, and what physical and chemical barriers could prevent the animals from ascending streams and successfully spawning.

The distribution of larval sea lampreys is affected most by the location of spawning sites, streamflow, water temperature, streambed, pollution, and downstream movement. However, as Hardisty and Potter (1971a) noted, it is difficult to delineate explicitly the physical and chemical characteristics of ammocoete habitats. The ecological factors which compose larval sea lamprey habitats are interrelated and tremendously complex. Contradictory findings and observations illuminate the need for more definitive studies in ammocoete ecology. Larval sea lampreys thrive in unpolluted, stable flowing streams with comparatively moderate summer temperatures (Stauffer and Hansen 1958; Manion and McLain 1971; Morman 1979); yet large numbers sometimes survive in polluted, intermittent, or warmwater habitats, based on observations made by personnel from the U.S. and Canadian control units. Both spawning adults and ammocoetes generally require flowing water; nevertheless, sea lampreys have spawned in still water (Skidmore 1959) and ammocoetes live in backwaters of streams and in lakes (Morman 1979). Although sea lamprey embryos can develop at low temperatures of 10.0–11.7°C (Manion and Hanson 1980), ammocoetes are absent from numerous cold-water streams. However, adults may not spawn in cold-water habitats (Applegate 1950). The effects of the many pollutants which occur in streams on embryonic and larval sea lampreys are enigmatic and need study. Spawning adults migrate through the heavily polluted main channels of rivers like the Saginaw, Grand, Kalamazoo, and St. Joseph, but no ammocoetes are produced in these habitats. Larval sea lampreys require soft substrates for burrowing, and are absent from streams with hard bottoms. Downstream movement causes the buildup of large ammocoete populations in the Great Lakes (Thomas 1962; Wagner and Stauffer 1962a) which may be a major source of recruitment to the parasitic population. Such migrations as well as lentic ammocoete populations need quantification, and should be a major consideration in selecting streams for installation of low-head barrier dams.

Such factors as water depth, illumination, food for ammocoetes, competition, predators, parasites, and pathogens do not seem to exert any direct, significant influence on the distribution of sea lampreys according to existing knowledge.

The plasticity of the sea lamprey's requirement for habitat and host along with its tremendous dispersal ability make it a difficult animal to study and to control. An integrated control effort, to which the Great Lakes Fishery Commission is committed, requires a knowledge of the where, when, and why of existing as well as potential sea lamprey distribution in the Great Lakes watershed. The ongoing efforts to clean up the lakes and their tributaries and to improve the salmonid fisheries are providing more and better lamprey habitat in the streams and an abundance of preferred prey in the lakes. Control efforts will probably remain directed for the most part at lampreys in the stream environment, be they spawning-run adults or larvae, but the growing emphasis on the development of alternatives other than the use of lampricides places a greater importance on the need for understanding the mechanisms that have influenced sea lamprey dispersal. For control to be effective it must be done on a large geographic scale.

When the many voids in our knowledge of the sea lamprey's ecology — some of which have been mentioned or alluded to in this paper — are filled, improved control at less cost, control schemes that are more acceptable from an environmental viewpoint, and perhaps the eradication of this pest from all or major parts of the Great Lakes may be attainable.

Applegate, V. C. 1950. Natural history of the sea lamprey, *Petromyzon marinus*, in Michigan. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 55: 237 p.

1961. Downstream movement of lampreys and fishes in the Carp Lake River, Michigan. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 387: 71 p.

Applegate, V. C., and C. L. Brynildson. 1952. Downstream movement of recently transformed sea lampreys, *Petromyzon marinus*, in the Carp Lake River, Michigan. Trans. Am. Fish. Soc. 81(1951): 275–290.

Applegate, V. C., and B. R. Smith. 1951. Movement and dispersion of a blocked spawning run of sea lampreys in the Great Lakes. Trans. 16th N. Am. Wildl. Conf. p. 243–251.

Aron, W. I., and S. H. Smith. 1971. Ship canals and aquatic ecosystems. Science 174(4004): 13–20.

Bailey, R. M. 1959. Parasitic lampreys (*Ichthyomyzon*) from the Missouri River, Missouri and South Dakota. Copeia 1959: 162–163.

Battle, H. I., and K. Hayashida. 1965. Comparative study of the intraperitoneal alimentary tract of parasitic and nonparasitic lampreys from the Great Lakes region. J. Fish. Res. Board Can. 22: 289–312.

Baxter, E. W. 1957. Lamprey distribution in streams and rivers. Nature 180: 1145.

Beamish, F. W. H. 1973. Oxygen consumption of adult *Petromyzon marinus* in relation to body weight and temperature. J. Fish. Res. Board Can. 30: 1367–1370.

1974. Swimming performance of adult sea lamprey, *Petromyzon marinus*, in relation to body weight and temperature. Trans. Am. Fish. Soc. 103: 355–358.

Beeton, A. M. 1963. Limnological survey of Lake Erie, 1959 and 1960. Great Lakes Fish. Comm. Tech. Rep. 6: 32 p.

1969. Changes in the environment and biota of the Great Lakes, p. 150–187. *In* Eutrophication: causes, consequences, correctives. Nat. Acad. Sci., Washington, D.C.

Blum, J. L. 1956. The ecology of river algae. Bot. Rev. 22: 291–341.

Budd, J. 1954. Lake Huron and Lake Superior lamprey scar counts, 1954, p. 14–18. *In* Great Lakes Fish. Committee, Minutes Annual Meeting, Nov. 30, 1954, St. Louis, MO.

Christie, W. J. 1973. A review of the changes in the fish species composition of Lake Ontario. Great Lakes Fish. Comm. Tech. Rep. 23: 65 p.

Christie, W. J., and D. P. Kolenosky. 1980. Parasitic-phase of the sea lamprey (*Petromyzon marinus*) in Lake Ontario. Can. J. Fish. Aquat. Sci. 37: 2021–2038.

Churchill, W. S. 1947. The brook lamprey in the Brule River. Trans. Wisc. Acad. Sci. Arts Lett. 37: 337–346.

Creaser, C. W. 1950. Non-feeding attachment of the sea lamprey (*Petromyzon marinus*). Anat. Rec. 108(3): 1 p.

Creaser, C. W., and C. S. Hann. 1929. The food of larval lampreys. Mich. Acad. Sci. Arts Lett. 10: 433–436.

Dodge, D. P. 1963. Survey of the Welland Ship Canal for sea lampreys (*Petromyzon marinus* L.). Fish. Res. Board Can., Manuscr. Rep. Ser. (Biol.) 745: 31 p.

Dryer, W. R. 1966. Bathymetric distribution of fish in the Apostle Islands region of Lake Superior. Trans. Am. Fish. Soc. 95: 248–259.

Erkkila, L. F. 1962. Lamprey control and research in the United States. Annual Rep. Great Lakes Fish. Comm., Ann Arbor, MI. p. 25–39.

Farmer, G. J., F. W. H. Beamish, and P. F. Lett. 1977. Influence of water temperature on the growth rate of the landlocked sea lamprey (*Petromyzon marinus*) and the associated rate of host mortality. J. Fish. Res. Board Can. 34: 1373–1378.

Fogelin, P. 1972. Studier över drift av larver och nymetamorfoserade ungar av flodnejonöga (*Lampetra fluviatilis* L.) i. Indais-älvan och Ricklean. Report from Ricklea Field Station. No. 20. (Information from this paper taken from Sjoberg 1980.)

Fothergill, C. (n.d.). Memoirs and illustrations of natural history in various parts of the British Empire. (Clendenan volume) Roy. Ont. Mus. (call number R.B., M.S. F661, No. 3). (Information from this paper taken from Lark 1973.)

GAGE, S. H. 1893. The lake and brook lampreys of New York especially those of Cayuga and Seneca lakes. The Wilder Quarter-Century Book. p. 421–493.

1928. The lampreys of New York State — life history and economics, p. 158–191. *In* A biological survey of the Oswego River system. Suppl. 17th Annu. Rep. N.Y. Conserv. Rep. 1927: 371 p.

GAYLORD, W. E., AND B. R. SMITH. 1966. Treatment of East Bay, Alger County, Michigan, with toxaphene for control of sea lampreys. U.S. Bur. Sport Fish. Wildl. Invest. Fish Control 7: 7 p. (Resour. Publ. 11)

GOODE, G. B. 1884. The lampreys — Petromyzontidae. Fishery Industry of the U.S. p. 677–681.

GREAT LAKES BASIN COMMISSION. 1976. Great Lakes basin framework study. Great Lakes Basin Comm. Rep. Append. C9: Commercial Navigation. 154 p.

GREAT LAKES FISHERY COMMISSION. 1961–76. Annual reports of the Great Lakes Fishery Commission, Ann Arbor, MI.

HAEDRICH, R. L. 1977. A sea lamprey from the deep ocean. Copeia 1977: 767–768.

HANSEN, M. J., AND D. W. HAYNE. 1962. Sea lamprey larvae in Ogontz Bay and Ogontz River, Michigan. J. Wildl. Manage. 26: 237–247.

HARDISTY, M. W. 1961. Studies on an isolated spawning population of the brook lamprey, *Lampetra planeri*. Ecology 30: 339–355.

HARDISTY, M. W., AND I. C. POTTER. 1971a. The biology, ecology, and growth of larval lampreys, p. 85–125. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London and New York.

1971b. The general biology of adult lampreys, p. 127–206. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London and New York.

HARRIS, H. W., AND J. S. LEVEY. [ed.] 1975. Welland Ship Canal, p. 2952. *In* The New Columbia Encyclopedia, 4th ed. Columbia Univ. Press, New York and London.

HARTMAN, W. L. 1973. Effects of exploitation, environmental changes, and new species on the fish habitats and resources of Lake Erie. Great Lakes Fish. Comm. Tech. Rep. 22: 43 p.

HODGES, J. W. 1972. Downstream migration of recently transformed sea lampreys before and after treatment of a Lake Michigan tributary with a lampricide. J. Fish. Res. Board Can. 29: 1237–1240.

HUBBS, C. L., AND K. F. LAGLER. 1974. Fishes of the Great Lakes region. Univ. Mich. Press, Ann Arbor, MI. 213 p.

HUBBS, C. L., AND M. B. TRAUTMAN. 1937. A revision of the lamprey genus *Ichthyomyzon*. Misc. Publ. Mus. Zool. Univ. Mich. 35: 109 p.

HUNN, J. B., AND W. D. YOUNGS. 1980. Role of physical barriers in the control of sea lamprey (*Petromyzon marinus*). Can. J. Fish. Aquat. Sci. 37: 2118–2122.

HYNES, H. B. N. 1970. The ecology of running waters. Univ. Toronto Press, Toronto, Ont. 555 p.

JOHNSON, B. G. H. 1958. Underwater examination of ships for hitchhiking lamprey at the Sault Ste. Marie lock. Fish. Res. Board Can., Biol. Sta. London, Ont., Annu. Rep. 1957–58, Append. 24. p. 73.

1969. Some statistics of the populations of parasitic-phase sea lampreys in the Canadian waters of the Great Lakes. Proc. 12th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res. p. 45–52.

JOHNSON, B. G. H., AND W. C. ANDERSON. 1980. Predatory-phase sea lampreys (*Petromyzon marinus*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37: 2007–2020.

JOHNSON, W. E. 1958. Density and distribution of young sockeye salmon (*Oncorhynchus nerka*) throughout a multibasin lake system. J. Fish. Res. Board Can. 15: 961–982.

KAINUA, K. J., AND T. VALTONEN. 1980. Distribution and abundance of European river lamprey (*Lampetra fluviatilis*) larvae in three rivers running into Bothnian Bay, Finland. Can. J. Fish. Aquat. Sci. 37: 1960–1966.

LARK, J. G. E. 1973. An early record of the sea lamprey (*Petromyzon marinus*) from Lake Ontario. J. Fish. Res. Board Can. 30: 131–133.

LAWRIE, A. H. 1970. The sea lamprey in the Great Lakes. Trans. Am. Fish. Soc. 99: 766–775.

LAWRIE, A. H., AND J. F. RAHRER. 1973. Lake Superior — a case history of the lake and its fisheries. Great Lakes Fish. Comm. Tech. Rep. 20: 55 p.

LEACH, J. M., AND S. J. NEPSZY. 1976. The fish community in Lake Erie. J. Fish. Res. Board Can. 33: 622–638.

LEACH, W. J. 1940. Occurrence and life history of the northern brook lamprey *Ichthyomyzon fossor* in Indiana. Copeia 1: 21–34.

1946. Oxygen consumption of lampreys, with special reference to metamorphosis and phylogenetic position. Physiol. Zool. 19: 365–374.

LEWIS, S. V. 1980. Respiration of lampreys. Can. J. Fish. Aquat. Sci. 37: 1711–1722.

MACEY, D. J., AND I. C. POTTER. 1978. Lethal temperatures of ammocoetes of the Southern Hemisphere lamprey, *Geotria australis* Gray. Environ. Biol. Fish. 32: 241–243.

MAITLAND, P. S. 1980. Review of the ecology of lampreys in northern Europe. Can. J. Fish. Aquat. Sci. 37: 1944–1952.

MANION, P. J. 1967. Morphological abnormalities among lampreys. Copeia 1967: 680–681.

1968. Production of sea lamprey larvae from nests in two Lake Superior streams. Trans. Am. Fish. Soc. 97: 484–486.

1969. Evaluation of lamprey larvicides in the Big Garlic River and Saux Head Lake. J. Fish. Res. Board Can. 26: 3077–3087.

MANION, P. J., AND L. H. HANSON. 1980. Spawning behavior and fecundity of lampreys from the upper three Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1635–1640.

MANION, P. J., AND A. L. MCLAIN. 1971. Biology of larval sea lampreys (*Petromyzon marinus*) of the 1960 year class, isolated in the Big Garlic River, Michigan, 1960–65. Great Lakes Fish. Comm. Tech. Rep. 16: 35 p.

MANION, P. J., AND B. R. SMITH. 1978. Biology of larval and metamorphosing sea lampreys, *Petromyzon marinus*, of the 1960 year class in the Big Garlic River, Michigan, Part II, 1966–72. Great Lakes Fish. Comm. Tech. Rep. 30: 35 p.

MCCAULEY, R. W. 1963. Lethal temperatures of the developmental stages of the sea lamprey, *Petromyzon marinus* L. J. Fish. Res. Board Can. 20: 483–490.

MCLAIN, A. L. 1952. Diseases and parasites of the sea lamprey, *Petromyzon marinus*, in the Lake Huron basin. Trans. Am. Fish. Soc. 81: 94–100.

MILLER, F. G. 1952. Surface temperatures on the Great Lakes. J. Fish. Res. Board Can. 9: 328–376.

MOORE, H. H., F. H. DAHL, AND A. K. LAMSA. 1974. Movement and recapture of parasitic-phase sea lampreys (*Petromyzon marinus*) tagged in the St. Marys River and lakes Huron and Michigan, 1963–67. Great Lakes Fish. Comm. Tech. Rep. 27: 19 p.

MOORE, H. H., AND L. P. SCHLEEN. 1980. Changes in spawning runs of sea lamprey (*Petromyzon marinus*) in selected streams of Lake Superior after chemical control. Can. J. Fish. Aquat. Sci. 37: 1851–1860.

Moore, J. W. 1972. Food selection, and consumption by larval sea lamprey, *Petromyzon marinus* Linnaeus, and American brook lamprey, *Lampetra lamottenii* (Lesueur). M.S. thesis, Univ. Guelph, Guelph, Ont. 55 p.

Moore, J. W., and F. W. H. Beamish. 1973. Food of larval sea lamprey (*Petromyzon marinus*) and American brook lamprey (*Lampetra lamottei*). J. Fish. Res. Board Can. 30: 7–15.

Moore, J. W., and J. M. Mallatt. 1980. Feeding of larval lamprey. Can. J. Fish. Aquat. Sci. 37: 1658–1664.

Morman, R. H. 1979. Distribution and ecology of lampreys in the Lower Peninsula of Michigan, 1957–75. Great Lakes Fish. Comm. Tech. Rep. 33: 59 p.

Morris, R. 1980. Blood composition and osmoregulation in ammocoete larvae. Can. J. Fish. Aquat. Sci. 37: 1665–1679.

Pearce, W. A., R. A. Braem, S. M. Dustin, and J. J. Tibbles. 1980. Sea lamprey (*Petromyzon marinus*) in the Lower Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1802–1810.

Pearson, R. L. 1957. Sea lamprey migrations by attachment to ships, p. 37–41. *In* Fish. Res. Board Can., Biol. Sta. Tech. Unit, London, Ont., Annu. Rep. 1956–57. Append. N.

Piavis, G. W. 1962. Exposure of several developmental stages of the sea lamprey, *Petromyzon marinus*, to selective larvicides. Copeia 1962: 652–653.

1971. Embryology, p. 361–400. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London and New York.

Piavis, G. W., and J. H. Howell. 1975. Effects of 3-trifluoromethyl-4-nitrophenol (TFM) on developmental stages of the sea lamprey. U.S. Fish Wildl. Serv. Invest. Fish Control 64: 8 p.

Pletcher, F. T. 1963. The life history and distribution of lampreys in the Salmon and certain other rivers in British Columbia, Canada. M.S. thesis, Univ. British Columbia, Vancouver, B.C. 195 p.

Potter, I. C. 1970. The life cycles and ecology of Australian lampreys of the genus *Mordacia*. J. Zool. London 61: 487–511.

Potter, I. C., and F. W. H. Beamish. 1975. Lethal temperatures in ammocoetes of four species of lampreys. Acta Zool. 56: 85–91.

Potter, I. C., B. J. Hill, and S. Gentleman. 1970. Survival and behaviour of ammocoetes at low oxygen tensions. Exp. Biol. 53: 59–73.

Potter, I. C., and M. J. Rogers. 1972. Oxygen consumption in burrowed and unburrowed ammocoetes of *Lampetra planeri* (Bloch). Comp. Biochem. Physiol. 41A: 427–432.

Pycha, R. L., and G. R. King. 1975. Changes in the lake trout population of southern Lake Superior in relation to the fishery, the sea lamprey, and stocking, 1950–70. Great Lakes Fish. Comm. Tech. Rep. 28: 34 p.

Randall, D. J. 1972. Respiration, p. 287–306. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2. Academic Press, London and New York.

Reynolds, W. W., and M. E. Casterlin. 1978. Behavioral thermoregulation by ammocoete larvae of the sea lamprey (*Petromyzon marinus*) in an electronic shuttlebox. Hydrobiologia (Abstr.) 61: 145–147.

1979. Photokinetic responses and diel activity of sea lamprey (*Petromyzon marinus*) ammocoete larvae. J. Fish. Biol. 14: 425–428.

Rugen, P. C. 1977. Summary report on Oswego River surveys. Great Lakes Fish. Comm., Rep. of Interim Meeting, Dec. 1977: 181–183.

Schroll, F. 1959. Zur Ernahrungsbiologie der Steirischen ammocoten *Lampetra planeri* (Bloch) und *Eudontomyzon danfordi* (Regan). Int. Rev. Gesamten Hydrobiol. 44: 395–429.

Schuldt, R. J., and R. Goold. 1980. Changes in the distribution of native lampreys in Lake Superior tributaries in response to sea lamprey (*Petromyzon marinus*) control, 1953–77. Can. J. Fish. Aquat. Sci. 37: 1872–1885.

Schultz, L. P. 1930. The life history of *Lampetra planeri* (Bloch), with a statistical analysis of the rate of growth of the larvae from western Washington. Occas. Pap. Mus. Zool. 221: 35 p.

Scott, W. E., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fish. Res. Board Can. 184: 966 p.

Sjöberg, K. 1980. Ecology of the European river lamprey (*Lampetra fluviatilis*) in northern Sweden. Can. J. Fish. Aquat. Sci. 37: 1974–1980.

Skidmore, J. F. 1959. Biology of spawning-run sea lamprey (*Petromyzon marinus*) in the Pancake River, Ontario. M.Sc. thesis, Univ. Western Ont., London, Ont. 87 p.

Smith, B. R. 1971. Sea lampreys in the Great Lakes of North America, p. 207–247. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London and New York.

Smith, B. R., and R. A. Braem. 1975. Sea lamprey control in the United States, p. 36–52. *In* Annu. Rep. Great Lakes Fish. Comm. (Append. C 1973), Ann Arbor, MI.

Smith, B. R., and O. R. Elliott. 1953. Movement of parasitic-phase sea lampreys in lakes Huron and Michigan. Trans. Am. Fish. Soc. 82: 123–128.

Simth, B. R., and E. L. King, Jr. 1970. Lamprey control in the United States, p. 29–40. *In* Annu. Rep. Great Lakes Fish. Comm. (Append. C 1969), Ann Arbor, MI.

Smith, B. R., and A. L. McLain. 1962. Estimation of the brook and sea lamprey ammocoete populations of three streams. Great Lakes Fish. Comm. Tech. Rep. 4: 18 p.

Smith, B. R., and J. J. Tibbles. 1980. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936–78. Can. J. Fish. Aquat. Sci. 37: 1780–1801.

Smith, S. H. 1968. Species succession and fishery exploitation in the Great Lakes. J. Fish. Res. Board Can. 25: 667–693.

1978. Lake Michigan's native fish face struggle with invaders. The Fisherman 30(2): 13 p. (Marine Publ. Co., Grand Haven, MI)

Starrett, W. C., W. J. Harth, and P. W. Smith. 1960. Parasitic lampreys of the genus *Ichthyomyzon* in Illinois. Copeia 4: 337–346.

Stauffer, T. M., and M. J. Hansen. 1958. Distribution of sea lamprey ammocoetes in Michigan tributaries of Lake Superior, 1954–57. Mich. Dep. Conserv., Inst. Fish. Res. Misc. Publ. 11: 25 p.

Sterba, G. 1962. Die Neunaugen (Petromyzonidae). Handb. Binnenfisch. Mitteleurop. 3: 263–352. (Transl. from German by R. W. McCauley, 138 p.)

Surface, H. A. 1899. Removal of lampreys from the interior waters of New York. Rep. Comm. Fish. Game Forest. p. 191–245.

Teeter, J. 1980. Pheromone communication in sea lampreys (*Petromyzon marinus*): implications for population management. Can. J. Fish. Aquat. Sci. 37: 2123–2132.

Thomas, M. L. H. 1960. A modified anchor dredge for collect: ing burrowing animals. J. Fish. Res. Board Can. 19-591–594.

1962. Observations on the ecology of ammocoetes of *Petromyzon marinus* L. and *Entosphenus* (*Lampetra*) *lamottei* (LeSueur) in the Great Lakes watershed. M.S. thesis, Univ. Toronto, Toronto, Ont. 214 p.

1963. Studies on the biology of ammocoetes in streams. Fish. Res. Board Can. 742: 143 p.

Tibbles, J. J. 1967. Lamprey control experiment in Canada, p. 41–46. *In* Annu. Rep. Great Lakes Fish. Comm. (Append. B 1966), Ann Arbor, MI.

Trautman, M. B. 1949. The invasion, present status, and life history of the sea lamprey in the waters of the Great Lakes, especially the Ohio waters of Lake Erie. Franz Theodore Stone Laboratory, Put-In-Bay, OH. 9 p.

1957. The fishes of Ohio. Ohio State Univ. Press, Columbus, OH. 683 p.

Tuunainen, P., E. Ikonen, and H. Auvinen. 1980. Lampreys and lamprey fisheries in Finland. Can. J. Fish. Aquat. Sci. 37: 1953–1959.

U.S. Department of Commerce. 1974. Great Lakes Pilot. U.S. Dept. Commerce, National Oceanic and Atmospheric Admin., Detroit, MI. 645 p.

Valtonen, T. 1980. European river lamprey (*Lampetra fluviatilis*) fishing and lamprey populations in some rivers running into the Bothnian Bay, Finland. Can. J. Fish. Aquat. Sci. 37: 1967–1973.

Veatch, J. D. 1953. Soils and land of Michigan. Mich. State College Press, East Lansing, MI. 241 p.

Vladykov, V. D. 1949. Quebec lampreys (Petromyzonidae). I. List of species and their economical importance. Dept. Fish. Province of Quebec Contrib. 26: 67 p.

1952. Distribution des lamproies (Petromyzonidae) dans la province de Quebec. Dept. Pecheries, Prov. Quebec, Contr. 36: 85–123.

Wagner, W. C., and T. M. Stauffer. 1962a. The population of sea lamprey larvae in East Bay, Alger County, Michigan. Pap. Mich. Acad. Sci. Arts Lett. 47: 235–245.

1962b. Sea lamprey larvae in lentic environments. Trans. Am. Fish. Soc. 91: 384–387.

Wigley, R. L. 1959. Life history of the sea lamprey of Cayuga Lake, New York. U.S. Fish Wildl. Serv. Fish. Bull. 59: 561–617.

Wilson, F. H. 1955. Lampreys in the Lake Champlain basin. Am. Midland Nat. 54: 163–172.

Wilson, K. A., and K. Ronald. 1967. Parasite fauna of the sea lamprey (*Petromyzon marinus* Von Linne) in the Great Lakes region. Can. J. Zool. 45: 1083–1092.

Effects of Temperature on Metamorphosis and the Age and Length at Metamorphosis in Sea Lamprey (*Petromyzon marinus*) in the Great Lakes[1]

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PURVIS, H. A. 1980. Effects of temperature on metamorphosis and the age and length at metamorphosis in sea lamprey (*Petromyzon marinus*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1827–1834.

Sea lamprey (*Petromyzon marinus*) ammocoetes of known age were confined in three locations to determine the effects of temperature on the incidence of metamorphosis. Sixty ammocoetes were held in each of Lake Superior, the Big Garlic River, and in an aquarium at room temperature for each of 4 yr. The highest incidence of metamorphosis (75–100%) occurred at 20–21°C (aquarium), an intermediate rate (46–76%) at 14–16°C (Big Garlic River), and the lowest (5–10%) at 7–11°C (Lake Superior). Density appeared to be the dominant factor in regulating the length of larval and transformed sea lampreys. Mean lengths of larval and transformed sea lampreys increased markedly after stream treatments with selective lampricides. Prediction of lengths at which metamorphosis occurs in re-established populations of sea lampreys is uncertain because of variability in growth rates. Initial metamorphosis in a year-class is dependent on growth rates of ammocoetes. Because of wide variation in growth rates, metamorphosis may begin at age III among fast-growing populations and not until age VII among slow-growing populations.

Key words: Petromyzon marinus, sea lamprey; metamorphosis, age, length, Great Lakes

PURVIS, H. A. 1980. Effects of temperature on metamorphosis and the age and length at metamorphosis in sea lamprey (*Petromyzon marinus*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1827–1834.

Afin de mesurer les effets de la température sur l'incidence de la métamorphose, des ammocoètes de grande lamproie marine (*Petromyzon marinus*) d'âge connu ont été confinés à trois endroits. Soixante ammocoètes ont été maintenus à chacun des trois sites suivants : lac Supérieur, rivière Big Garlic et aquarium à température ambiante, sur une période de 4 ans. L'incidence maximale de métamorphose (75–100%) se produisit à 20–21°C (aquarium), un taux intermédiaire (46–76%) à 14–16°C (rivière Big Garlic) et incidence minimale (5–10%) à 7–11°C (lac Supérieur). La densité semble être le facteur dominant qui contrôle la longueur des lamproies larvaires et métamorphosées. La longueur moyenne des lamproies larvaires et métamorphosées augmente notablement après traitement du cours d'eau à des lampricides sélectifs. À cause de la variabilité des taux de croissance, il est difficile de prédire la longueur à laquelle la métamorphose se produit chez des populations rétablies de grandes lamproies marines. La métamorphose initiale chez une classe d'âge dépend du taux de croissance des ammocoètes. Par suite d'une grande variabilité du taux de croissance, la métamorphose peut commencer à l'âge III chez des populations à croissance rapide, alors que chez des populations à croissance lente, elle ne commencera qu'à l'âge VII.

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USE of the selective lampricide, 3-trifluoromethyl-4-nitrophenol (TFM), has drastically reduced the sea lamprey (*Petromyzon marinus*) population throughout the Great Lakes (Smith 1971). Chemical treatments of tributaries of Lake Superior began in 1958, and were later extended to tributaries of Lakes Michigan and Huron in 1960 and Ontario in 1971.

Electrical barriers, operated on eight tributaries of Lake Superior each year from 1958 to 1978, monitored changes in the population of adult sea lampreys (Smith and Tibbles 1980). The number of adults captured at the barriers from 1973 to 1978 declined 93% from the record high catch of 51 000 in 1961. Although there has been no direct evaluation of the decline of adult sea lampreys in the other lakes, reduced numbers of ammocoetes and transformed lampreys, reduced scarring rates, and increased survival of salmonids indi-

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cate large reductions in adult sea lamprey populations.

The success of the sea lamprey control program depends on the treatment of lamprey-infested streams before sea lampreys metamorphose and migrate into the Great Lakes. To increase efficiency of chemical treatments and reduce costs, accurate knowledge of the age at initial metamorphosis of sea lampreys is necessary to provide a base to establish the intervals between chemical treatments.

Information on three aspects of sea lamprey metamorphosis having relevance to the sea lamprey control program is provided in this paper. Included are the length and age of sea lampreys at metamorphosis, and the effects of temperature on this process.

Effects of Three Different Regimes on Metamorphosis in Sea Lampreys

Limited data are available on the effects of temperature on metamorphosis of lampreys. Presumably, streams that meet the basic temperature requirements of lampreys for spawning, hatching, growth, and survival to transformation size also meet the temperature requirements for transformation.

In one laboratory experiment, sea lampreys of metamorphosing size were exposed to an average temperature of 13°C from July 1 to September 30, and thereafter to temperatures of 6–7°C through April 27, but they did not complete metamorphosis (Manion and Stauffer 1970). Lampreys that had entered various stages of metamorphosis had neither emerged from the sand substrate nor attained mouth lengths of 8% of the total body length by April 27, when the experiment was terminated. It is unknown whether these lampreys were capable of feeding parasitically. Although the temperature was only 14°C (one Celsius degree higher) in the control group, some lampreys emerged December 16 and fed February 8. Evidence was inconclusive that temperature was the only factor in the uncompleted metamorphosis.

Another effect of temperature on metamorphosis of lampreys was reported by Potter (1970). The onset of transformation in the Australian lamprey (*Mordacia mordax*), under laboratory conditions, was delayed 4–5 wk at 15°C when compared with another group held at 22–25°C. Potter (1980) also suggested that the degree of change, rather than the precise temperature, was important in the timing of transformation.

In the course of investigating the location and abundance of larval sea lamprey populations in Lake Superior, it became apparent that transformed lampreys were extremely scarce in offshore waters of Lake Superior, although transformed lampreys were routinely collected in shallow bays off the mouths of some Lake Superior tributaries. Large ammocoetes (>130 mm long) were collected in depths of 12 m and up to 1.2 km offshore in Lake Superior, but transformed sea lampreys were virtually nonexistent, suggesting that perhaps the deep, cold water of Lake Superior inhibited or prevented transformation of sea lamprey ammocoetes. If transformation does not occur in offshore areas of Lake Superior, then these populations of ammocoetes will not contribute to the parasitic phase and can be disregarded.

The limited data available on the effects of temperature on metamorphosis prompted a field study of the effect of Lake Superior water temperature on metamorphosis. This was conducted at the Marquette Sea Lamprey Control Station from 1974 to 1977 to determine the incidence of metamorphosis in sea lampreys exposed to three temperature regimes.

Materials and Methods

Ammocoetes of the 1960 year-class were collected each spring (mainly in mid-April) in an inclined trap in the Big Garlic River (Manion and McLain 1971; Manion and Smith 1978). They were transported alive to the Marquette Sea Lamprey Control Station until placement in mid-May. A considerable proportion of the test animals were expected to metamorphose because of the large size and old age (14 yr) of the ammocoetes (Table 1). Manion and Smith (1978) noted that 40% of samples of large larvae captured at the trap in the spring and held in live cages metamorphosed in 1967, 1968, and 1970.

In each of 4 yr, selected groups of 60 ammocoetes were confined in each of three areas: Lake Superior at a depth of 11 m, the Big Garlic River in a backwater, and an aquarium at room temperature at Marquette. A total of 180 ammocoetes were divided randomly into three groups of 60 each and placed in the three locations on May 9 in 1974 and 1975, on May 10 in 1976, and on May 25 in 1977.

One group of 60 ammocoetes was placed in a closed system aquarium 27 × 6 × 3 cm which contained a substrate of washed beach sand, 75 mm deep. The aquarium was filled with 15 cm of water from Lake Superior and supplied with an aerator. The ammocoetes were not fed. The other two groups of 60 ammocoetes were subdivided into groups of 20 larvae and placed in wire mesh cages (three at each site) in Lake Superior (lake group) and the Big Garlic River (river group). The cages were 9.5 × 4.7 × 4.7 cm. Scuba divers placed the cages at a depth of 11 m in Lake Superior and added 75 mm of sand. A recording thermograph was installed at all three sites. Three cages were placed in 30 cm of water in a backwater area of the Big Garlic River and 75 mm of substrate was added. The substrate consisted mainly of sand with small amounts of detritus and silt. Before ammocoetes were introduced into the cages they were anesthetized in M.S. 222, measured to the nearest millimetre, and weighed to the nearest 0.1 g.

Ammocoetes were usually examined for evidence of transformation each year about July 1, mid-September, and the end of October. The criterion used for completion of metamorphosis was the length of the mouth (oral disc) to body length ratio (Manion and Stauffer 1970).

Results

The field study suggested that transformation is related to temperature (Table 1). The highest percentage of animals entering metamorphosis each year was observed in the aquarium at room temperatures (20–

TABLE 1. Mean length (mm) of 60 sea lamprey ammocoetes of the 1960 year-class at various ages exposed to three temperature regimes, and the percentage that transformed, 1974–77. (Percentage transformation was based on the number of lampreys that survived at each location. Average water temperature (°C) from mid-May to July 31 in parentheses.)

	1974		1975		1976		1977	
	Age XIV		Age XV		Age XVI		Age XVII	
Location	%	Mean length	%	Mean length	%	Mean length	%	Mean length
Lake Superior	5 (7)	152	10 (11)	152	8 (11)	149	10 (10)	141
Big Garlic River	46 (14)	153	51 (16)	151	76 (14)	146	63 (16)	142
Aquarium	75 (20)	151	84 (21)	154	100 (20)	148	95 (21)	143

21°C). An intermediate rate occurred in the control group in the Big Garlic River (14–16°C) and the lowest percentage was found in the Lake Superior group (7–11°C). The incidence of transformation of ammocoetes in the river group was 5–9 times greater (average, 7) than the lake group over the 4-yr period, and larvae in the aquarium transformed at a rate 8–15 times (average, 11) greater than the lake group.

The percentage of ammocoetes transforming in the river group and the aquarium increased each year from 1974 to 1976 (Table 1). An increase might be expected because the ammocoetes used in the study each year were 1 yr older than the previous year. Age groups increased from XIV in 1974 to XVII in 1977. The slight decrease in transformation rates in 1977 (Table 1) may have resulted from the use of slightly smaller larvae in 1977. No trend towards increased transformation rates with age was observed in the Lake Superior group. It would appear that the cold temperature suppressed transformation regardless of the length or age of the ammocoetes.

A larger mean length in lampreys that metamorphosed than in lampreys that did not metamorphose would indicate a greater rate of metamorphosis in larger lampreys than in smaller lampreys. However, data from the river group showed that in 3 of the 4 yr of the study, the mean length of the transformed and untransformed lampreys was similar (Table 2).

Similarity in mean lengths between transformed and larval lampreys in 1974–76 indicated there was no tendency for the larger lampreys to metamorphose at a greater rate than the smaller ones. It also showed that a relatively old age and a large length did not guarantee metamorphosis of all lampreys. Although there was no tendency for the longer lampreys to metamorphose in this unique sample of lampreys, i.e. old age and large size, data from the Big Garlic River in earlier years (Manion and Smith 1978) demonstrated that the longer larvae metamorphose first.

Larvae that were introduced into Lake Superior from 1974 to 1977 and failed to metamorphose each year were immediately returned to Lake Superior and observed for another year. Surprisingly, the percentage of transformation increased markedly in this group after an additional year of exposure in Lake Superior. The transformation rate of the 1974 group increased to 63% (20 of 32), the 1975 group to 44% (16 of 36), the 1976 group to 33% (6 of 18), and the 1977 group to 17% (8 of 48). These data suggest that ammocoetes that migrate into Lake Superior in the spring transform at minimal rates during their first summer, but acclimatization for an additional year results in much

TABLE 2. Length of transformed and larval sea lampreys from the 1960 year-class of ammocoetes caged in the Big Garlic River.

	Transformed			Larval		
		Length (mm)			Length (mm)	
Date	Number	Mean	Range	Number	Mean	Range
Sept. 13, 1974	26	149	127–162	31	147	120–170
Sept. 15, 1975	23	145	125–160	22	145	128–164
Sept. 13, 1976	45	145	126–158	14	144	132–161
Sept. 30, 1977	37	149	125–175	22	141	123–163

TABLE 3. Percentage of mouth length to total length of transformed sea lampreys exposed to three temperature regimes, 1974–77. (Range in temperature from mid-May to July 31 each year. Number of sea lampreys measured in parentheses.)

Location and temperature range	1974		1975		1976		1977
	Sept. 9–13	Oct. 29–30	Sept. 15–17	Oct. 28–30	Sept. 13–14	Nov. 1–3	Sept. 27–30
Lake Superior 7–11°C	2.6 (3)	6.1 (3)	4.1 (5)	7.7 (6)	2.9 (1)	5.0 (4)	3.8 (6)
Big Garlic River 14–16°C	5.1 (26)	6.7 (10)	5.9 (23)	8.3 (22)	5.5 (45)	7.1 (44)	7.9 (37)
Aquarium 20–21°C	—	—	6.9 (38)	9.3 (18)	7.1 (59)	8.4 (59)	8.8 (57)

higher transformation rates. Most important, these data show that ammocoetes can survive and metamorphose in the cold, offshore water of Lake Superior at a depth of 11 m. However, transformed sea lampreys were not observed long enough to determine whether metamorphosis was completed and whether the lampreys would eventually feed parasitically.

Morphological changes associated with metamorphosis also were related to water temperature. Manion and Stauffer (1970) based four stages of transformation primarily on the condition of the mouth, or oral disc. One criterion they used for completion of metamorphosis was when mouth lengths of lampreys were 8–9% of the total body length. In the present study, the development of the mouth showed marked variability at different temperature regimes (Table 3). During transformation, the relative size of the mouth increased fastest in the aquarium, at an intermediate rate in the Big Garlic River, and slowest in Lake Superior. Mouth lengths of lampreys from the lake group had not reached 8% of the body length by the end of each October, when observations were terminated. However, the ratio of mouth to body lengths in the aquarium exceeded 8% by September or October each year.

The decreased rate of transformation in the lake and river groups, when compared with the aquarium group, suggests that the critical factors that influence metamorphosis may be effective in a period of about 6 wk before metamorphosis. Before ammocoetes were introduced into Lake Superior and the Big Garlic River, they were held at 19°C for a period of 3 wk after their capture in 1974–76 and for 5 wk in 1977. This exposure to an elevated temperature in an aquarium for a period of 3–5 wk, about 1½–2 mo before metamorphosis normally begins in streams, was not enough to produce a significant rate of transformation in the Lake Superior ammocoetes.

Ammocoetes reintroduced into the Big Garlic River were also exposed to elevated temperatures for 3–5 wk from mid-April to May, but failed to metamorphose at rates similar to the aquarium group. These data are a further indication that temperatures necessary to trigger metamorphosis probably occur within a 5- to 6-wk period in June and early July.

Metamorphosis in the Great Lakes region begins in early to mid-July and is not initiated after August (Manion and Stauffer 1970). In the present study, metamorphosis in a few lampreys confined in Lake Superior was not evident until after September 15. No delayed metamorphosis was noted in the other two groups. The earliest evidence of transformation was detected in the aquarium group on June 28, when two lampreys were noted with fused lips and prominent eyespots.

The factors that trigger metamorphosis are unknown. Despite the wide differences in temperatures in streams throughout the Great Lakes region, there is a remarkable synchrony in the onset of metamorphosis. With few exceptions, the earliest stages in metamorphosis have been observed only between early July and late August.

Although none of the variables such as substrate, atmospheric pressure, photoperiod, dissolved oxygen, and water chemistry, which might affect transformation, were controlled in this study, there appears to be little doubt that the difference in the thermal regimes was a significant factor in producing the different incidence of transformation among the three groups. The study indicates that a greater proportion of ammocoetes exposed to temperatures of about 20°C from mid-April to July will transform than larvae exposed to temperatures of 10 and 15°C. Further controlled laboratory experiments are needed to define the upper, lower, and optimum temperatures required for transformation, and to determine whether larvae exposed to lowered temperatures, similar to Lake Superior, can complete metamorphosis and eventually feed parasitically.

Lengths of Sea Lamprey at Metamorphosis

Mean lengths of sea lampreys at metamorphosis in tributaries of the Great Lakes vary between 124 and 177 mm (Manion and Stauffer 1970; Purvis 1979). Manion and Stauffer (1970) reported that mean lengths of metamorphosed sea lampreys in 11 tributaries of Lake Superior and 8 tributaries of Lake Michigan were 145 and 136 mm, respectively. Mean lengths of metamorphosed lampreys collected in Lake Superior tributaries ranged from 124 to 160 mm and from 124 to 150 mm in Lake Michigan tributaries.

Transformed sea lampreys with mean lengths in excess of 160 mm were usually associated with reductions in population density of larvae, either as a result of chemical treatments or limited recruitment to larval populations. Sea lamprey ammocoetes that escape chemical treatments (residuals) are larger at transformation than those collected during the first chemical treatment. Mean lengths in excess of 160 mm and as long as 177 mm have been reported for these populations that survive chemical treatments (Smith 1971; Hodges 1972; Purvis 1979). For example, Purvis (1979) reported that the mean length of transformed lampreys collected during the initial treatments of six streams tributary to Lake Superior was 140 mm (range, 133–147). The mean length of lampreys that survived the original treatments and were collected as transformed lampreys in later treatments was 166 mm (range, 160–173), a 19% increase. The mean length of residual transformed lampreys collected in a third treatment of the Huron River (Lake Superior) increased from 163 to 177 mm, an additional 9% increase (Fig. 1).

Mean lengths of larval and transformed sea lampreys in areas of reduced population density also have been reported (Applegate 1961; Manion and Smith 1978; Purvis 1979). Metamorphosed sea lampreys recovered in a low density area above the falls in the Ocqueoc River (Lake Huron) during the initial chemical treatment in 1968 had a mean length of 161 mm, whereas, below the falls, where annual recruitment occurred (high density), transformed lampreys had a mean length of 135 mm (Purvis 1979). The large mean length of the larvae that had not metamorphosed (150 mm; range, 96–185) indicated that only sporadic recruitment to the population had occurred above the falls on the Ocqueoc River. Increased growth of fish following decreases in abundance is a common phenomenon reported for many species of fish. The increased length of larval and transformed lampreys resulting from reduced population density suggests that density is a dominant factor in regulating the length of larvae and transformed sea lampreys.

Several investigators believed density was a dominant factor in controlling growth of sea lamprey larvae (Manion and McLain 1971; Manion and Smith 1978; Purvis 1979). Length–frequency distribution of sea lamprey ammocoetes throughout the Great Lakes area shows only a small percentage of ammocoetes larger than 160 mm (Applegate 1950, 1961; Stauffer 1956; Wigley 1959; Hardisty 1961; Thomas 1962; Manion and McLain 1971; Lowe 1972, Lowe et al. 1973; O'Boyle and Beamish 1977; Manion and Smith 1978; Purvis 1979). Large ammocoetes over 160 mm were uncommon in samples of lampreys collected during the initial treatments of many Great Lakes streams (unpublished data). Applegate (1950) collected only four larvae (0.1%) over 160 mm in a sample of 3486 ammocoetes from the Ocqueoc River (Lake Huron), and 7 ammocoetes occurred in a sample of 2634 (0.3%) in Carp Lake River, a tributary of Lake Michigan (Applegate 1961). A combination of population density, including competition with native lampreys, and the filter-feeding existence of ammocoetes probably are factors regulating the size at which sea lampreys transform.

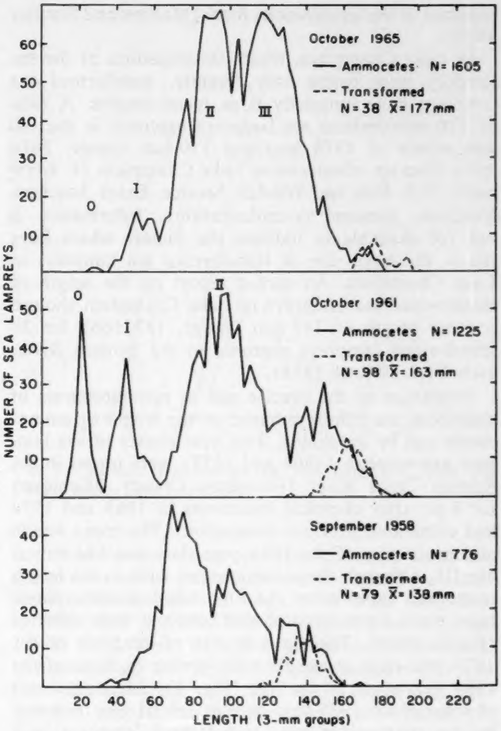

FIG. 1. Length distribution of sea lampreys collected in three chemical treatments of the Huron River, Lake Superior.

Since the mean lengths of transformed sea lampreys from anadromous populations in New Brunswick, Canada, ranged from 119 to 130 mm, Potter et al. (1978) have suggested that there was a tendency for the anadromous sea lampreys to enter metamorphosis at a smaller size than its landlocked derivative. However, the possibility cannot be excluded that these differences are due to dissimilar rates of growth resulting from environmental factors. Mean lengths of transformed sea lampreys in some tributaries of Lakes Superior and Michigan were nearly as small (124 mm long) as those reported in the anadromous form (Manion and Stauffer 1970).

In Lake Champlain, where investigations of the sea lamprey were begun only recently, transformed sea lampreys have unusually large mean lengths. A total of 170 transformed sea lampreys captured in the fall and winter of 1978 averaged 170 mm (range, 147–205) from six tributaries of Lake Champlain (J. Gersmehl, U.S. Fish and Wildlife Service, Essex Junction, Vermont, personal communication). Information is not yet available to indicate the factors which have led to the large size of transformed sea lampreys in Lake Champlain. An earlier report on the length of transformed sea lampreys in Lake Champlain showed a mean length of 147 mm (range, 133–166) for 30 transformed lampreys captured in the Salmon River, New York (Wilson 1955).

Prediction of the precise age at metamorphosis of individual sea lampreys based on the length of ammocoetes can be unreliable. Two year-classes of sea lamprey ammocoetes (1964 and 1975) were traced in the Salmon Trout River (Houghton County, Michigan) for 3 yr, after chemical treatments in 1963 and 1974 had eliminated previous populations. The mean length of ammocoetes of the 1964 year-class was 144 mm at age III. Although these ammocoetes were in the length range and captured at the time when metamorphosis takes place, no metamorphosed lampreys were collected (Purvis 1979). The mean lengths of lampreys of the 1975 year-class at age III were similar to those of the 1964 year-class at age III (Fig. 2). Metamorphosis of some of the 1975 year-class at age III was indicated by the recovery of nine transformed lampreys in a chemical treatment in October 1978. The apparent difference in the occurrence of metamorphosis of sea lampreys of similar ages and lengths in the Salmon Trout River emphasizes the variation in the life cycle of sea lampreys and the difficulty in predicting the length at metamorphosis of individual lampreys.

Age at Metamorphosis of Sea Lampreys

In the past, investigators relied on the length–frequency method to estimate age at metamorphosis of lampreys. Estimates of the age at metamorphosis of sea lampreys in the Great Lakes region varied from 3 to 7 yr (Gage 1928; Applegate 1950; Wigley 1959; Hardisty 1961; Lowe et al. 1973). Analysis of length-frequency data suggested that transformed sea lampreys belonged to only one age-group (Gage 1928; Applegate 1950; Wigley 1959). Ammocoetes as large as or larger than metamorphosed lampreys were presumed to be ammocoetes of a younger year-class and were in a "rest period" or phase of arrested growth and would transform the following year. However, large samples of ammocoetes of transformation size that failed to metamorphose were not observed over a number of successive years to confirm that the "rest period," when ammocoetes accumulate lipids, is only of 1 yr duration.

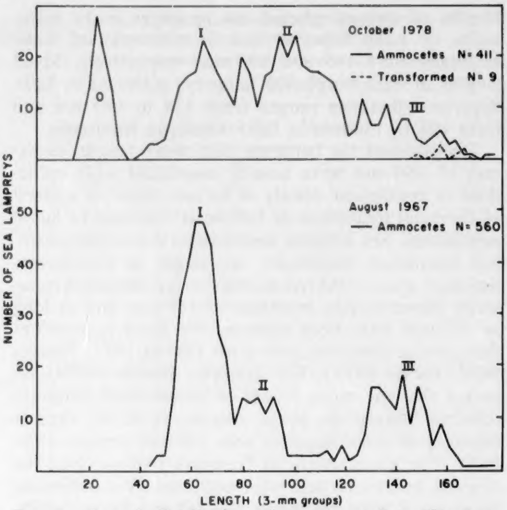

FIG. 2. Length distribution of age-groups 0 to III of sea lampreys from the Salmon Trout River, Houghton County, Lake Superior.

Criteria to age lampreys accurately are not available. Because lampreys lack scales, bones, or otoliths which are commonly used to age fish, it is impossible to verify estimates of age at metamorphosis, the number of age-groups present in a sample of transformed lampreys, or the concept of a "rest period."

Two studies were begun at the Marquette Sea Lamprey Control Station in 1960 to provide accurate knowledge on the age at metamorphosis of sea lampreys by monitoring known-age populations of ammocoetes. In the first study, a single year-class of ammocoetes was established by introducing sexually mature sea lampreys above a dam and series of falls in the Big Garlic River, a tributary of Lake Superior (Manion and McLain 1971; Manion and Smith 1978). A specially designed all-season trap (McLain and Manion 1967) was used to collect ammocoetes on which to base the age at metamorphosis of the population.

In the second study, larvae of known age were monitored in tributaries of Lakes Superior and Michigan after previous populations were eradicated by chemical treatments (Purvis 1979). These known-age populations were monitored several times annually until transformation was detected or imminent, and then the streams were chemically treated.

The results of these two studies provided basic data on the relationship between age and metamorphosis in newly established populations of sea lampreys. In the Big Garlic River study, ammocoetes of the 1960 year-class began metamorphosing in 1965 and larvae of this year-class were still present in 1978 (Manion and Smith 1978). Consequently, the life expectancy for some sea lampreys from the Big Garlic River was about 20 yr, which would include 18 yr in the larval stage and 12–20 mo in the parasitic stage before eventual spawning and death.

The study of known-age ammocoetes established after chemical treatments showed that the age at which the first ammocoetes entered metamorphosis occurred at age III among fast-growing larvae in large streams and not until age VII among slow-growing larvae in small streams. Generally, ammocoetes require 5 or more years of larval life before transformation (Purvis 1979). In contrast to the rapid growth and early age at metamorphosis in some newly established populations of sea lampreys, Potter (1980) suggested that the average age at metamorphosis is from 6 to 8 yr for old established populations of anadromous and landlocked sea lampreys.

The percentage of lampreys that metamorphose each year from a known-age class of sea lampreys varied from stream to stream. In the Big Garlic River, metamorphosed lampreys comprised less than 1% of the estimated larval population each year from age V to XI. The percentage of metamorphosed lampreys collected in reestablished populations was based on the ratio of transformed lampreys to the number of larvae as long as or longer than the smallest transformed lamprey. Initial transformation of lampreys of known age, established after chemical treatments in three Lake Michigan tributaries, was 0.2% at age VII in Hog Island Creek, 4% at age VII in Deadhorse Creek, and 4% at age V in Marblehead Creek. In two Lake Superior tributaries, 16% of 1117 sea lampreys transformed at age V in the Little Garlic River and 34% of 553 age IV lampreys transformed in the Potato River.

The fact that transformation occurs at an earlier age in streams where growth of ammocoetes is most rapid is consistent with the fact that the proportion of large lampreys entering metamorphosis is greater than in those rivers where growth is slow. A high ratio of transformed lampreys to larval lampreys at a young age would not be expected in streams in which the growth of larvae was slow. Based on the study of known-age populations of sea lampreys, it is now apparent that ammocoetes of a single year-class would not be expected to metamorphose simultaneously in a single year. On the other hand, the high rate of transformation and large size of age IV larvae in the Potato River (Fig. 3) would indicate a much shorter larval life than was found in the Big Garlic River.

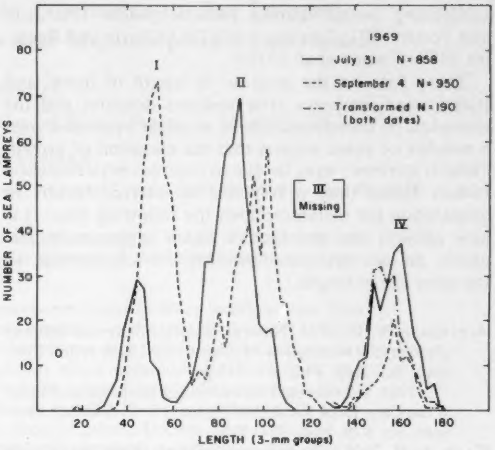

FIG. 3. Length distribution of sea lampreys from the Potato River, Lake Superior.

The concept of a "rest period" in ammocoetes was reviewed by Manion and Smith (1978). To determine whether the life cycle included a 1-yr rest period, a total of 551 larvae (age-group VIII) with a mean length of 138 mm (range, 127–164) were marked and released in the Big Garlic River. Although all marked larvae were within the length range of transformation, transformed lampreys were collected from this group over a 5-yr period. Of the 186 lampreys recaptured in the transformed stage, 49% were recaptured in 1968, 20% in 1969, 22% in 1970, 8% in 1971, and 1% in 1972. These data demonstrate that ammocoetes of a similar age and length will not automatically transform the following year. This study began 3 yr after the first transformed lampreys were collected in the Big Garlic River, and from these data Manion and Smith (1978) concluded that the concept of just a 1-yr rest period in ammocoetes before metamorphosis was erroneous.

Studies of know-age ammocoetes reestablished after chemical treatments also indicated that metamorphosis would extend over a period of years, once larvae reach transformation size (Purvis 1979). An increase in length of ammocoetes in the Potato River from July 31 to September 4, 1969, was noted in age I and II larvae, but no increase was observed in length of the IV group (Fig. 3). From July to September, the modal length of age I larvae increased from 44 to 53 mm, the II group from 89 to 101 mm, but the IV group decreased from 161 to 158 mm. These data indicate the IV group larvae had approached their maximum length, and growth had ceased. Although 34% of the sample of lampreys had metamorphosed, 66% of the ammocoetes as large as metamorphosed lampreys failed to metamorphose (Fig. 3). The cessation of growth of the IV group could be referred to as a "rest period," although a reduction in the population density could result in a resumption of growth as was noted in the Huron River after chemical treatment (Fig. 1).

Recent studies have suggested that although increases in length are halted before metamorphosis, this period is used to accumulate lipids necessary for an extended nonfeeding period during metamorphosis (Hardisty and Potter 1971; Lowe et al. 1973; O'Boyle and Beamish 1977; Youson et al. 1979).

These data on the increase in length of larval and transformed lampreys after reduced densities and the extension of transformation of a single year-class over a number of years suggest that the cessation of growth (length increase) may be due to external environmental factors rather than a response to internal factors in preparation for metamorphosis the following year. It is now obvious that the factors which trigger metamorphosis do not act simultaneously on ammocoetes of the same age or length.

APPLEGATE, V. C. 1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 55: 237 p.

1961. Downstream movement of lampreys and fishes in the Carp Lake River, Michigan. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 387: 71 p.

GAGE, S. H. 1928. The lampreys of New York State — life history and economics, p. 158–191. *In* A biological survey of the Oswego River system, Suppl. 17th Annu. Rep., N.Y. Conserv. Dep. 1927: 371 p.

HARDISTY, M. W. 1961. The growth of larval lampreys. J. Anim. Ecol. 30: 357–371.

HARDISTY, M. W., AND I. C. POTTER. 1971. The general biology of adult lampreys, p. 127–206. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London and New York.

HODGES, J. W. 1972. Downstream migration of recently transformed sea lampreys before and after treatment of a Lake Michigan tributary with a lampricide. J. Fish. Res. Board Can. 29: 1237–1240.

LOWE, D. R. 1972. Variations in body composition of pre-adult landlocked sea lamprey, *Petromyzon marinus* L., in relation to size and season. M.S. thesis, Univ. Guelph, Guelph, Ont., Canada. 78 p.

LOWE, D. R., F. W. H. BEAMISH, AND I. C. POTTER. 1973. Changes in the proximate body composition of the landlocked sea lamprey *Petromyzon marinus* (L.) during larval life and metamorphosis. J. Fish. Biol. 5: 673–682.

MANION, P. J., AND A. L. MCLAIN. 1971. Biology of larval sea lampreys (*Petromyzon marinus*) of the 1960 year-class, isolated in the Big Garlic River, Michigan, 1960–65. Great Lakes Fish. Comm. Tech. Rep. 16: 35 p.

MANION, P. J., AND B. R. SMITH. 1978. Biology of larval and metamorphosing sea lampreys, *Petromyzon marinus*, of the 1960 year-class in the Big Garlic River, Michigan, Part II, 1966–72. Great Lakes Fish. Comm. Tech. Rep. 30: 35 p.

MANION, P. J., AND T. M. STAUFFER. 1970. Metamorphosis of the landlocked sea lamprey, *Petromyzon marinus*. J. Fish. Res. Board Can. 27: 1735–1746.

MCLAIN, A. L., AND P. J. MANION. 1967. An all-season trap for downstream-migrating fish and other aquatic organisms. Prog. Fish-Cult. 29: 114–117.

O'BOYLE, R. N., AND F. W. H. BEAMISH. 1977. Growth and intermediary metabolism of larval and metamorphosing stages of the landlocked sea lamprey, *Petromyzon marinus* L. Environ. Biol. Fish. 2: 103–120.

POTTER, I. C. 1970. The life cycles and ecology of Australian lampreys of the genus *Mordacia*. J. Zool. 161: 487–511.

1980. Ecology of larval and metamorphosing lampreys. Can. J. Fish. Aquat. Sci. 37: 1641–1657.

POTTER, I. C., G. M. WRIGHT, AND J. H. YOUSON. 1978. Metamorphosis in the anadromous sea lamprey, *Petromyzon marinus* L. Can. J. Zool. 56: 561–570.

PURVIS, H. A. 1979. Variations in growth, age at transformation, and sex ratio of sea lampreys reestablished in chemically treated tributaries of the Upper Great Lakes. Great Lakes Fish. Comm. Tech. Rep. 35: 36 p.

SMITH, B. R. 1971. Sea lampreys in the Great Lakes of North America, p. 207–247. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London and New York.

SMITH, B. R., AND J. J. TIBBLES. 1980. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936–78. Can. J. Fish. Aquat. Sci. 37: 1780–1801.

STAUFFER, T. M. 1956. An investigation of the continued capture of downstream-migrating recently transformed sea lampreys in the downstream trap of a weir on Carp Lake River, Emmet County, 1955. Mich. Conserv. Inst. Fish. Res. Rep. 1474: 1–16.

THOMAS, M. L. H. 1962. Observations on the ecology of *Petromyzon marinus* L. and *Entosphenus lamottei* (Le Sueur) in the Great Lakes watershed. M.S.A. thesis, Univ. Toronto, Toronto, Ont. 170 p.

WIGLEY, R. L. 1959. Life history of the sea lamprey of Cayuga Lake, New York. U.S. Fish Wildl. Serv. Fish. Bull. 59: 561–617.

WILSON, W. H. 1955. Lampreys in the Lake Champlain basin. Am. Wildl. Nat. 54: 168–172.

YOUSON, J. H., J. LEE, AND I. C. POTTER. 1979. The distribution of fat in larval, metamorphosing, and young adult anadromous sea lampreys *Petromyzon marinus* L. Can. J. Zool. 57: 237–246.

Ecological Impacts of Lampricide Treatments on Sea Lamprey (*Petromyzon marinus*) Ammocoetes and Metamorphosed Individuals[1]

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Sea lamprey (*Petromyzon marinus*) ammocoetes are found in fewer locations now than before lampricide treatments began. Posttreatment reinfestation does not always occur in those tributaries previously infested. Abundance of ammocoetes and transformed individuals has declined in most watersheds with a few exceptions where density-dependent factors may have been influential. Increased growth was related to reduced density. Sex compositions of larval and metamorphosing populations were highly variable during initial lampricide treatments. Females predominated in some streams, males in others. Streams once dominated by males now favor females in residual and reestablished populations of larvae. The shift to femaleness in the larval populations has precipitated a similar shift in adult sea lamprey populations of the upper Great Lakes.

Key words: sea lamprey, ammocoetes, transformed, distribution, abundance, growth, sex composition

TORBLAA, R. L., AND R. W. WESTMAN. 1980. Ecological impacts of lampricide treatments on sea lamprey (*Petromyzon marinus*) ammocoetes and metamorphosed individuals. Can. J. Fish. Aquat. Sci. 37: 1835–1850.

Les ammocoètes de grande lamproie marine (*Petromyzon marinus*) se rencontrent maintenant à moins d'endroits qu'au début du traitement aux lampricides. La réinfestation après le traitement ne se produit pas toujours dans les tributaires infestés antérieurement. Les ammocoètes et les sujets transformés ont diminué d'abondance dans la plupart des bassins hydrographiques, à l'exception de quelques cas où des facteurs dépendant de la densité ont pu avoir une influence. Une croissance accrue est liée à une densité réduite. La proportion des sexes, chez les populations larvaires et en voie de transformation, était très variable au moment des applications initiales de lampricides. Dans certains cours d'eau, les femelles prédominaient, alors que dans d'autres c'était les mâles. Des cours d'eau jadis dominés par des mâles contiennent maintenant plus de femelles chez les populations résiduaires ou rétablies de larves. Ce glissement vers une plus forte proportion de femelles chez les populations larvaires a entraîné un glissement semblable chez les populations de grandes lamproies marines adultes des Grands Lacs supérieurs.

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THE first of a series of selective toxicants for the ammocoetes of sea lamprey (*Petromyzon marinus*) was discovered in 1956 and then field-tested. The most effective one, 3-trifluoromethyl-4-nitrophenol (TFM), was adopted for field use in 1958 (Applegate et al. 1958). Tests in 1963 revealed that a molluscicide increased the toxicity of TFM without significantly affecting its selectivity toward sea lampreys (Howell et al. 1964). This compound, 2′,5-dichloro-4′-nitrosalicylanilide (Bayer 73), has also been used extensively in the control program since 1965.

The objectives of this study were to ascertain and describe the demonstrable impacts that lampricide treatments have had on populations of sea lamprey ammocoetes and transformed individuals in streams. Changes in distribution, abundance, growth, and sex ratios are described.

Materials and Methods

Sea lamprey larvae and transformed individuals used in this study were collected in the course of stream surveys

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[1] This paper forms part of the Proceedings of the Sea Lamprey International Symposium (SLIS) convened at Northern Michigan University, Marquette, Michigan, July 30–August 8, 1979.

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and lampricide treatments. Most stream surveys were carried out with electroshockers. Early investigators used gasoline-powered, direct-current shockers as described by Pratt (1952). These were later replaced by alternating-current, backpack, electric converter units (Tibbles 1959; Braem and Ebel 1961), and recently by completely transistorized units that deliver pulsed, square-wave, direct current (Smith 1971). The transistorized model, a more efficient unit, has been used since 1968. Generally, teams of two spend from 30 to 60 min at each station and cover an area of 46–93 m^2. TFM and Bayer 73 have also been used where the effectiveness of electroshockers was limited by turbidity, deep water, or low conductivity. Most streams that have had sea lamprey populations are monitored annually to detect changes in distribution, abundance, and growth.

The backpack shockers are relatively ineffective for collecting and evaluating populations of metamorphosing lampreys (Manion and Smith 1978); however, other methods are available such as fyke nets and collecting baskets at water-intake structures. The shockers, nevertheless, remain the primary tool for collecting and evaluating lamprey populations in streams. Admittedly, abundance estimates thus obtained may be somewhat biased for a variety of reasons. The shockers have undergone several modifications and each has resulted in increased efficiency. Changes in personnel and consequent changes in collecting ability may also introduce bias into abundance estimates. More experienced personnel probably collect greater numbers of larvae in a given time period. Further, although not considered in this report, collecting conditions vary between treatments.

Smith et al. (1974) described the methodology for chemical control on Lake Superior streams and the procedures were essentially the same for other Great Lakes tributaries. Lamprey ammocoetes and transformed individuals were collected during and after chemical treatments with standard "riffle" fyke nets and dip nets. All lampreys collected during stream surveys and chemical treatments were preserved in 10% formalin and later identified, based on characteristics described by Vladykov (1960) and Purvis (1970).

Sex determinations for larvae and partially and fully metamorphosed lampreys were based on characteristics described by Applegate and Thomas (1965). Hardisty (1965) determined that the gonads of sea lamprey larvae are sexually differentiated when the ammocoete has reached a total length of 100 mm. Sex ratios of specimens less than 120 mm examined microscopically did not differ significantly from sex ratios of larvae greater than 120 mm, and since many large samples were available, an arbitrary minimum length of 120 mm was selected to permit rapid and accurate sexing. Sex of partially and fully metamorphosed sea lampreys was easily determined macroscopically since differences in size and color between the male and female gonads are even more pronounced than in the larvae.

Effects of Chemical Treatments on Distribution of Sea Lamprey Larvae

DISTRIBUTION IN THE GREAT LAKES

The Michigan Department of Natural Resources found sea lamprey larvae in 21 of 60 Michigan tributaries of Lake Superior examined in 1955–57 (Stauffer and Hansen 1958). Subsequent surveys by the U.S. Fish and Wildlife Service and the Department of Fisheries and Oceans of Canada located sea lamprey larvae in 147 Lake Superior streams, 86 in the United States and 61 in Canada.

The Michigan Department of Natural Resources also recovered sea lamprey ammocoetes in 20 of 27 tributaries to northern Lake Michigan in 1955–59 (Stauffer 1961). Later surveys by the U.S. Fish and Wildlife Service expanded the total to 117 Lake Michigan streams that contained sea lamprey larvae.

Surveys by the U.S. Fish and Wildlife Service and the Department of Fisheries and Oceans of Canada found sea lamprey larvae in 111 Lake Huron streams, 60 in the United States and 51 in Canada. Surveys in cooperation with the New York Department of Environmental Conservation found sea lamprey larvae in 51 Lake Ontario tributaries, 26 in the United States and 25 in Canada.

LAKE SUPERIOR STREAMS

Chemical treatment of streams tributary to Lake Superior began in 1958 when TFM was applied to 12 tributaries (Smith et al. 1974). The first four treatments were considered experimental and were conducted under the supervision of the Hammond Bay Biological Station (Applegate et al. 1961). Since then, 109 other streams have been treated at least once, and 57 have been treated five or more times (Table 1). Twenty-six streams have not been treated because sea lamprey populations have disappeared, or they contained relatively small numbers of ammocoetes.

Single applications of the lampricide apparently "eradicated" sea lamprey populations from 18 streams; reestablishment of sea lamprey ammocoetes, when it occurred, was minimal and not of a magnitude that warranted additional chemical treatments. Sea lamprey populations have disappeared from 11 other streams after two or more chemical treatments and were not present for the past 5 years or more. The 5-yr period was arbitrarily selected, and is not meant to imply that reestablishment will never recur in these streams. Sea lamprey ammocoetes were recovered in some streams after absences of more than 10 yr. It seems unlikely, however, that at present levels of control, such streams will contribute significantly to adult stocks.

Most of the streams without recruitment for 5 or more years have serious limiting factors as described by Smith et al. (1974). Some are streams with cold water, steep gradient, limited spawning grounds, little larval habitat, and physical barriers to upstream migration.

LAKE MICHIGAN STREAMS

Chemical treatment of Lake Michigan tributaries began in 1960 when TFM was applied to seven streams tributary to the north shore (Great Lakes Fishery Com-

TABLE 1. Summary of data on sea lamprey infestations and lampricide treatments of streams by lake and location. Asterisks identify streams in which sea lampreys were judged in 1978 to have been effectively "eradicated" in that few or none were observed after the year specified in the third column. (Increase (+), decrease (−), little or no change (0).)

Lake, jurisdiction, and stream	Total number of lampricide treatments	Year sea lampreys last observed	Change in size of habitat used
Superior			
Michigan			
Chippewa			
Waiska River	5		−
Pendills Creek	4		0
Grants Creek	2		0
Naomikong Creek*	1	1970	−
Ankodosh Creek	3		0
Galloway Creek	4		+
Tahquamenon River	6		+
Betsy River	6		−
Luce			
Three Mile Creek*	1	1962	−
Little Two-hearted River	6		−
Two-hearted River	6		−
Dead Sucker River	2		−
Alger			
Sucker River	13		−
Sable Creek	1		0
Sullivans Creek	4		−
Seven Mile Creek	3		0
Beaver Lake Outlet	10		−
Mosquito River*	4	1973	−
Miners River	5		+
Munising Falls Creek*	1	1969	−
Anna River*	1	1965	−
Furnace Creek	10		−
Five-mile Creek	4		−
Au Train River	10		−
Rock River	6		−
Deer Lake Outlet	2		−
Laughing Whitefish River	5		−
Sand River*	4	1972	−
Marquette			
Chocolay River	5		−
Carp River*	1	1963	−
Harlow Creek	12		+
Little Garlic River	6		+
Big Garlic River	12		+
Iron River	6		0
Salmon Trout River	5		+
Pine River*	3	1972	−
Huron River	6		0
Baraga			
Ravine River	8		+
Slate River	6		−
Silver River	11		+
Falls River	6		−
Six Mile Creek*	1	1963	−
Houghton			
Sturgeon River	11		+
Pilgrim River*	1	1966	−
McCallum Creek*	1	1964	−
Trap Rock River	1		+
Traverse River	8		+
Smiths Creek*	1	1964	−
Boston-Lily Creek*	1	1972	−
Salmon Trout River	6		0
Mud Lake Outlet*	4	1973	−
Graveraet River*	1	1963	−
Elm River	2		0
Keweenaw			
Little Gratiot River	3		+
Eliza Creek	7		−
Big Gratiot River	3		0
Washington Creek	1		+
Ontonagon			
Misery River	5		+
East Sleeping River	7		−
Firesteel River	5		+
Ontonagon River	8		+
Potato River	7		+
Cranberry River	6		+
Little Iron River	2		−
Union River*	1	1964	−
Gogebic			
Black River	2		0
Montreal River	1		−
Wisconsin			
Ashland			
Bad River	9		+
Bayfield			
Fish Creek (Eileen Twp.)	4		+
Raspberry River*	1	1963	−
Sand River	1		−
Reefer Creek*	1	1964	−
Fish Creek (Orienta Twp.)*	1	1964	−
Douglas			
Brule River	7		+
Poplar River	5		−
Middle River	5		+
Amnicon River	7		+
Nemadji River	7		−
Minnesota			
Lake			
Split Rock River	3		0
Gooseberry River	1		−
Cook			
Arrowhead River	5		0
Poplar River	1		−
Ontario			
Algoma			
East Davignon Creek*	3	1972	−
West Davignon Creek	6		+
Little Carp River	5		−
Big Carp River	5		−
Cranberry River	4		+
Goulais River	6		−
Stokeley River	6		+
Harmony River	5		−
Sawmill Creek*	3	1968	−
Chippewa River	10		0
Batchawana River	11		0
Sable River	13		+
Pancake River	6		+
Agawa River	4		0
Sand River*	4	1971	0
Michipicoten River	5		+
Dog River*	1	1963	−
Thunder Bay			
White River	4		0
Big Pic River	3		0
Little Pic River*	3	1972	−
Prairie River	3		0
Steel River	3		+
Pays Plat River*	2	1963	−
Big Gravel River	7		+
Little Gravel River	5		+
Cypress River	5		+
Jackfish River	5		+
Cash Creek	2		0
Nipigon River	3		+
Otter Cove Creek*	3	1971	−
Stillwater Creek	4		−
Black Sturgeon River	4		0
Wolf River	7		+
Pearl River	5		+
Blende Creek*	1	1964	−
McIntyre River*	2	1960	−
Neebing River*	1	1972	−
Kaministikwia River	7		−
Pigeon River	4		+
Cloud River	3		0
Michigan			
Michigan			
Mackinac			
Brevort River	6		−
Paquin Creek	5		−
Davenport Creek*	1	1970	−
Hog Island Creek	4		0
Sucker Creek	1		0
Black River	6		+

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[a] Unofficial name.

TABLE 1 (*Continued*)

Lake, jurisdiction, and stream	Total number of lampricide treatments	Year sea lampreys last observed	Change in size of habitat used
Mile Creek	4		0
Millecoquins River	8		–
Rock River	3		0
Crow River	2		–
Catarac River	2		–
Point Patterson Creek	3		–
Hudson Creek	5		0
Swan Creek*	1	1961	–
Schoolcraft			
Milakokia River	5		+
Bulldog Creek	4		–
Gulliver Lake Outlet	4		–
Marblehead Creek	5		–
Manistique River	3		+
Southtown Creek	1		–
Johnson Creek	4		0
Deadhorse Creek	4		–
Bursaw Creek	5		+
Parent Creek	5		0
Poodle Pete Creek	4		0
Delta			
Valentine Creek	5		–
Little Fishdam River	3		–
Fishdam River	5		–
Sturgeon River	5		–
Ogontz River	6		+
Squaw Creek	5		+
Hock Creek	2		0
Whitefish River	7		+
Rapid River	6		+
Tacoosh River*	2	1966	–
Days River	5		–
Portage Creek	3		–
Ford River	7		–
Sunny Brook	2		–
Bark River	4		–
Menominee			
Cedar River	4		–
Sugar Creek	3		+
Arthur Bay Creek*	2	1970	–
Rochereau Creek*	1	1963	–
Johnson Creek*	1	1963	–
Bailey Creek	3		0
Beattie Creek	3		0
Springer Creek	4		–
Menominee River	1		0
Emmet			
Carp Lake River	4		0
Big Stone Creek	3		0
Big Sucker Creek*	3	1972	–
Wycamp Lake Outlet	2		0
Charlevoix			
Horton Creek	8		0
Boyne River	5		0
Porter Creek	5		0
Jordan River	5		–
Monroe Creek*	2	1972	–
Loeb Creek*	3	1971	–
McGeach Creek	3		–
Antrim			
Elk River	3		0
Grand Traverse			
Yuba Creek*	2	1971	–
Acme Creek*	1	1973	–
Mitchell Creek	3		–
Boardman River	5		+
Leelanau			
Goodharbor Creek	4		0
Crystal River	2	1972	–
Benzie			
Platte River	5		–
Betsie River	5		0
Manistee			
Big Manistee River	7		0
Little Manistee River	4		0
Mason			
Gurney Creek	2		0
Lincoln River	4		0
Pere Marquette River	4		–
Oceana			
Pentwater River	4		0
Stoney Creek	2		0
Muskegon			
Flower Creek	1		+
White River	4		+
Big Bear Creek	2		–
Muskegon River	5		+
Black Creek*	2	1970	–
Norris Creek	2		0
Ottawa			
Grand River	3		0
Pigeon River*	1	1964	–
Pine Creek*	1	1964	–
Allegan			
Gibson	1		0
Kalamazoo River	6		–
Allegan 3 Creek*[a]	1	1965	–
Allegan 4 Creek[a]	2		–
Van Buren			
Black River	4		0
Brandywine Creek*	2	1973	0
Rogers Creek	2		0
Berrien			
St. Joseph River	4		0
Galien River	4		0
Wisconsin			
Marinette			
Little River	2		0
Peshtigo River	2		0
Oconto			
Oconto River	1		–
Pensaukee River	2		–
Door			
Ephraim Creek*	1	1963	–
Hibbards Creek	3		0
Whitefish Bay Creek*	1	1969	–
Lilly Bay Creek*	1	1963	–
Bear Creek	2		–
Door 23 Creek[a]	2		0
Kewaunee			
Ahnapee River*	1	1964	–
Three Mile Creek	3		–
Kewaunee River	1		0
Manitowoc			
East Twin River	1		+
Indiana			
LaPorte			
State Creek	4		0
Trail Creek	1		+
Porter			
Donns Creek*,[a]	1	1966	–
Burns Ditch	3		+
Huron			
Michigan			
Chippewa			
Little Munuscong River	5		–
Munuscong River	5		–
Carlton Creek	3		0
Canoe Lake Outlet*	1	1970	–
Caribou Creek	4		0
Bear Lake Outlet	2		0
Carr Creek	3		0
Joe Straw Creek	2		–
Albany Creek	5		+
Trout Creek	5		–
Mackinac			
Beavertail Creek	4		–
Prentiss Creek	5		–
McKay Creek	4		+
Ceville Creek	1		–
Hessel Creek	2		–
Steeles Creek	3		0
Nunns Creek	2		–
Pine River	4		+
McCloud Creek	1		–
Carp River	5		–
Martineau Creek	3		–

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[a] Unofficial name.

TABLE 1 (*Concluded*)

Lake, jurisdiction, and stream	Total number of lampricide treatments	Year sea lampreys last observed	Change in size of habitat used
Cheboygan			
266-20 Creek[a]	1		0
Little Black River*	1	1972	−
Cheboygan River	2		0
Meyers Creek	2		0
Laperell Creek	2		0
Pigeon River	3		0
Maple River	3		−
Sturgeon River	3		+
Elliot Creek	5		0
Greene Creek	4		0
Grass Creek	3		0
Presque Isle			
Mulligan Creek	4		0
Grace Creek	4		0
Black Mallard Creek	5		+
Seventeen Creek	1		−
Ocqueoc River	5		−
Johnny Creek	1		0
Schmidt Creek	3		−
Trout River	4		0
Swan Creek	3		−
Alpena			
Middle Lake Outlet*	1	1967	−
Squaw Creek*	1	1967	0
Devils Creek	3		0
Alcona			
Black River*	1	1970	−
Iosco			
Au Sable River	3		0
Pine River	3		−
Tawas Lake Outlet	3		0
Sims Creek	1		0
Silver Creek	2		0
Arenac			
East Au Gres River	4		0
Au Gres River	3		0
Rifle River	3		0
Midland			
Saginaw River (Bluff Creek)	1		+
Ontario			
Algoma			
Root River	5		−
Garden River	4		−
Bar Creek*	1	1966	−
Gawas Creek	5		0
Two Tree River*	2	1972	−
Richardsons Creek	3		−
Watsons Creek	4		0
Gordons Creek	5		0
Browns Creek	5		+
Kaskawong River	4		−
H-65[a]	2		+
H-68[a]	3		0
McBeth Creek	2		−
Thessalon River	3		0
Livingston Creek	2		0
Mississagi River	4		+
Blind River*	1	1971	−
Lauzon River	3		+
Spragge River*	2	1967	−
Serpent River	5		0
Sudbury			
Spanish River	3		−
Wanapitei River	3		0
Manitoulin			
Kagowong River	1		0
Silver Lake Creek	3		0
Sand Creek	2		0
Mindemoya River	3		+
Manitou River	3		−
Blue Jay Creek	3		−
Kaboni Creek	3		0
Chikanishing River	4		−
Parry Sound			
Nisbet Creek*	1	1972	−
Still River	4		−
Magnetawan River	4		+
Naiscoot River	3		0
Boyne River	4		−
Squirrel Creek*	1	1972	0
Muskoka			
Muskoka River	1		0
Simcoe			
Sturgeon River	4		−
Hog Creek	1		−
LaFontaine Creek*	2	1968	−
Nottawasaga River	4		−
Pretty River*	1	1972	−
Silver Creek	4		−
Grey			
Bothwell Creek	2		0
Sydenham River*	2	1972	−
Bruce			
Sauble River	2		0
Saugeen River	1		−
Huron			
Bayfield River*	1	1970	−
Ontario			
New York			
Jefferson			
Stony Creek*	1	1972	−
South Sandy Creek	2		+
Oswego			
Skinner Creek	4		+
Lindsey Creek	4		+
Blind Creek	3		−
Little Sandy Creek	4		0
Deer Creek	3		−
Salmon River	4		−
Grindstone Creek	3		+
Snake Creek	1		−
Sage Creek	2		+
Little Salmon River	2		0
Butterfly Creek*	1	1972	−
Catfish Creek	2		−
Rice Creek*	1	1972	−
Ninemile Creek	1		0
Cayuga			
Sterling Creek	2		−
Wayne			
Blind Sodus Creek	1		0
Wolcott Creek	2		−
Sodus Creek	3		+
Third Creek*,[a]	1	1972	−
First Creek[a]	1		−
Ontario			
Wentworth			
Ancaster Creek	2		+
Halton			
Bronte Creek	3		+
Oakville Creek	2		−
Peel			
Credit River	2		+
Ontario			
Rouge River	1		+
Duffin Creek	4		+
Carruthers Creek	1		−
Lynde Creek	3		−
Oshawa Creek	3		0
Durham			
Harmony-Farewell Creek	3		+
Bowmanville-Soper Creek	3		0
Wilmot Creek	3		+
Graham Creek	3		−
Port Britain Creek	2		0
Gage Creek*	1	1972	−
Northumberland			
Cobourg Creek	3		−
Grafton Creek	2		−
Shelter Valley Creek	3		−
Lakeport Creek	2		−
Salem Creek	2		−
Butler Creek	2		0
Smithfield Creek	2		0
Hastings			
Trent (Mayhew) Creek	2		0
Addington			
Salmon River	3		+

[a] Unofficial name.

mission 1960). Since then, 105 other streams were treated at least once, and 28 were treated five or more times (Table 1). Five streams were not treated because populations of sea lamprey ammocoetes disappeared spontaneously.

Again, sea lamprey populations have been effectively "eradicated" from 13 streams by single applications of lampricide. They disappeared in nine other streams after two or more chemical treatments, and no reestablishment has been observed for the past 5 years or more. Generally, the limiting factors mentioned for Lake Superior tributaries where sea lampreys have not reappeared also apply to these streams.

LAKE HURON STREAMS

Chemical treatment of Lake Huron tributaries began in 1957–58 when field tests were conducted on Little Billies (Elliot) and Carp (Black Mallard) creeks, respectively (Great Lakes Fishery Commission 1958). The control program was expanded to Lake Huron in 1960, and although limited funds dictated an interruption between 1963 and 1965, treatments have occurred regularly since 1966. A total of 103 streams were treated at least once, and 15 were treated five or more times (Table 1). Nine streams have not been treated, because populations of sea lamprey ammocoetes disappeared spontaneously.

Sea lamprey populations were eradicated from 11 streams by single applications of lampricide. They disappeared in four other streams after two or more treatments and no reestablishment has been observed for the past 5 years or more.

LAKE ONTARIO STREAMS

Sea lamprey control expanded to Lake Ontario in 1971 when lampricide was applied to 23 streams on the Canadian shore (Great Lakes Fishery Commission 1971). Twenty-three other Lake Ontario tributaries were treated subsequently, and 19 were treated three or more times (Table 1). Five have not been treated, and only five show no evidence of reestablishment for the past 5 years or more.

CHANGES IN DISTRIBUTIONAL PATTERNS WITHIN STREAMS

Chemical treatments also caused obvious changes in the dispersal of larvae in main streams and their tributaries. The total length of a stream inhabited by sea lamprey ammocoetes may vary considerably between treatments. The number of infected tributaries in individual streams does not always remain the same, and shifts in distributional patterns occur in streams that are regularly reinfected.

These changes are not clearly understood, but may be influenced by water temperature. Streams that would normally be too cold for sea lamprey use might be warmed by impounded water such as that created by beaver dams. Another may be the exposure of suitable spawning material because of flooding, by gravel from road construction being deposited in the stream, or by shifts in stream flows. Changes in water quality may also influence changes in distributional patterns. Sterba (1962) reported that although migrating adult lampreys pass through polluted portions of streams, even slight pollution may destroy larval populations.

In Lake Superior streams, distribution of larvae decreased in 49% of the streams, increased in 32%, and did not change in 19% (Table 1). Thirty of 39 streams in which distribution of larvae increased had electrical barriers in operation for various periods of time. Their removal, in many instances, may have allowed spawning sea lampreys access to suitable areas that were not otherwise available.

Distribution of larvae within streams of Lake Michigan was also reduced in 49%, increased in 14%, and unchanged in 37%. Ten of 16 streams that showed increases in distribution of sea lamprey ammocoetes had electrical barriers in operation for various periods of time. Three had dams that were removed, altered, or apertures developed that rendered them ineffective as barriers to spawning sea lampreys. Distribution of larvae in Lake Huron tributaries decreased in 46%, increased in 12%, and did not change in 42%. The changes were not as pronounced in Lake Ontario streams where the control program is relatively recent — the initial treatments were begun in 1971. Distribution of larvae decreased, in 48%, increased in 30%, and did not change in 22% of these streams.

Generally, the declines in total length of a stream inhabited by sea lamprey ammocoetes have not followed the sequential order of treatments; however, in some streams progressive decreases occurred with successive chemical treatments. Three streams tributary to the west shore of Lake Michigan have experienced such declines after every chemical treatment (Table 2). The total decrease from the initial to the most recent stream survey was 29% in the Ford River, 31% in the Cedar River, and 26% in the Bark River. Whether this trend will continue and is influenced in part by factors other than the control program, e.g. water temperature and stream flow during the spawning migration, is not known.

While the declines in these streams seem substantial, they have not greatly simplified the logistics of lampricide applications. Sea lamprey larvae recently were discovered in high water channels, oxbows, and backwaters that are not effectively penetrated by lampricides. It is necessary to treat these areas separately in conjunction with regularly scheduled chemical treatments. The Ford and Cedar rivers contained 171 and 70 of these areas, respectively, during the last lampricide applications of these two streams.

Another change in distributional pattern within individual streams has been an apparent shift of sea lamprey populations from one tributary to another (Table 2). This shift is particularly evident in tributaries of

TABLE 2. Total length of stream in kilometres inhabited by sea lampreys with respect to successive chemical treatments.

Lake and stream	Initial survey	Before-treatment number 2	3	4	5
Lake Michigan					
Ford River	237	232	230	219	170
Cedar River	168	142	138	116	—
Bark River	38	34	34	28	—
Lake Huron					
Pine River					
Biscuit Creek	0	7	7	15	—
Trout Brook	6	6	5	0	—

the Pine River, a stream that flows into Lake Huron in Mackinac County, Michigan, a relatively remote portion of Michigan's Upper Peninsula. Biscuit Creek is a tributary that joins the main stream 28.5 km upstream from the mouth, and Trout Brook is a tributary of Biscuit Creek that joins 3.9 km upstream of its junction with the Pine River. Biscuit Creek was not infected upstream of its junction with Trout Brook before the original chemical treatment of the Pine River system. Recent surveys have shown that a major portion of Biscuit Creek is now infected. Trout Brook supported a spawning run of sea lampreys as early as 1946 (Applegate 1950), and early chemical treatments confirmed that it contained substantial numbers of sea lamprey ammocoetes. Sea lampreys are no longer present in Trout Brook. Again, no obvious changes in the physical character of the stream were observed.

An additional change in distributional pattern has been the occurrence in streams of isolated populations of sea lamprey larvae. Original surveys generally revealed a continuous distribution of sea lamprey ammocoetes from the mouth to the upstream limits. It has been observed more frequently in the past few years that sea lamprey ammocoetes are restricted to short stretches and none are found upstream or downstream of these limited areas. A comparison of the original and most recent distribution of sea lamprey ammocoetes in Hibbards Creek illustrates this change (Fig. 1). Hibbards Creek is a small stream tributary to the west shore of Lake Michigan in Door County, Wisconsin. Various types of barriers operated in this stream captured as many as 12 640 adult sea lampreys in 1951 (Great Lakes Fishery Commission 1961). The number had declined to 783 by 1963, the last year of operation.

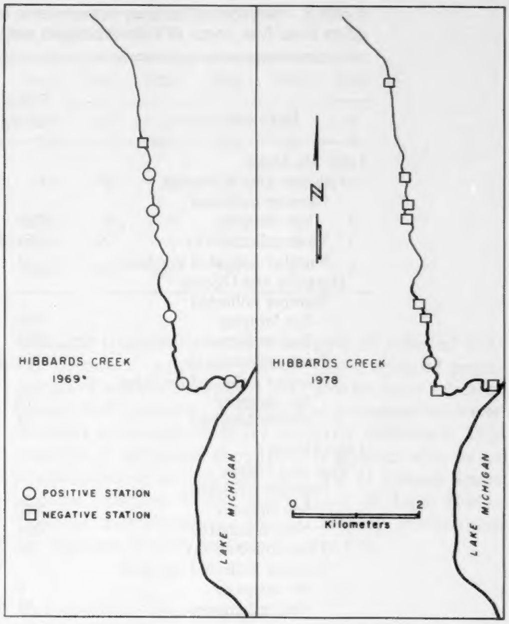

FIG. 1. Distribution of sea lamprey ammocoetes in Hibbards Creek, 1969 and 1978.

In many instances, the occurrence of these isolated populations may be influenced by the frequency of chemical applications. Ammocoetes have not had enough time to drift into or repopulate areas that were previously infected. Several streams were placed on an accelerated treatment schedule in the early 1970s because they contained lentic or other areas not reached by conventional methods; they had potential to produce transformed individuals earlier than most; and they frequently contained residual sea lampreys after successive chemical treatments. It seems probable, however, that reduced populations of adult stocks have also been influential in creating these isolated populations. It may be necessary to devote more time and effort to detect these populations to further the success of the control program.

Effects of Lampricide Treatments on Abundance

SEA LAMPREY AMMOCOETES

The first attempt to estimate the size of the ammocoete population in a stream tributary to the Great Lakes was made by Hansen and Hayne (1962) in the Ogontz River, a small tributary to the north shore of Lake Michigan. They estimated the total number of sea lamprey ammocoetes to be 136 800. Later, Smith and McLain (1962) estimated that 170 570 were destroyed by the initial chemical treatment. Unfortunately, quantitative data from subsequent treatments are not available.

Smith (1971), however, demonstrated a 46% reduction in numbers collected between the first and second treatments of 36 north shore tributaries to Lake Michigan, but only a 2% reduction in 11 Lower Michigan streams. A similar examination of data from

TABLE 3. Number of lamprey ammocoetes collected with backpack shockers and collecting effort from four rivers of Lake Michigan and two of Lake Huron.

Lake and river	Initial survey	Before-treatment number			
		2	3	4	5
Lake Michigan					
Fishdam and Whitefish					
Number collected					
Sea lamprey	1386	262	1462	699	733
Time collected (h)	54.8	20.8	142.7	83.7	109.2
Number collected per hour	25	13	10	8	7
Sturgeon and Ogontz					
Number collected					
Sea lamprey	960	275	292	1113	1835
Native lamprey	2265	304	535	473	352
Time collected (h)	64.4	54.3	69.8	73.9	68.8
Number collected per hour					
Sea lamprey	15	5	4	15	27
Native lamprey	35	6	8	6	5
Lake Huron					
Pine and Carp					
Number collected					
Sea lamprey	840	1063	815	1129	—
Native lamprey	3064	1337	226	309	—
Time collected (h)	98.2	106.9	62.8	79.9	—
Number collected per hour					
Sea lamprey	9	10	13	14	—
Native lamprey	31	13	4	4	—

34 streams tributary to Lake Ontario revealed only a 3% reduction.

Abundance of sea lamprey ammocoetes also declined in several Canadian tributaries to Lake Huron. The total number of sea lamprey ammocoetes collected during initial chemical treatments was 18 094, declined to 16 152 during second treatments, and further to 11 253 during third-round treatments. The numbers of larvae collected per hour declined from 31 to 24 and 20, respectively. Abundance declined in 11 streams, increased in 2, and changed little in 2. Other attempts to standardize collection data from chemical treatment samples have been largely unsuccessful because of changes in methods and shortage of personnel.

In addition to those streams previously mentioned where sea lamprey ammocoetes have not become reestablished after one or more chemical treatments, declines in abundance occurred in several streams that are regularly reinfected after successive treatments. Collections taken with backpack shockers have demonstrated such declines in two streams tributary to the north shore of Lake Michigan (Table 3). The Fishdam and Whitefish rivers have a combined total length of 497 km (Brown 1944), and sea lamprey ammocoetes have been recovered from a major portion of this distance. They are regularly reinfected after successive chemical treatments, and year-classes are established annually. Although the streams were surveyed extensively outside of the original distribution, the results reported herein refer only to collections from portions that were previously inhabited by sea lamprey ammocoetes. Collections from immediate posttreatment surveys are not included, and the others are not separated by year-classes.

The total number of sea lamprey ammocoetes collected per hour from the Fishdam and Whitefish rivers before original treatments decreased 72%, compared with the number collected during most recent stream surveys. The downward trend is evident despite a refinement in technique that occurred between the second and third chemical treatments. Presumably, the relatively large areas examined, the length of time expended, and the number of times most stations were repetitively examined would tend to minimize the effects of other variables. Similarly, the total number of sea lamprey ammocoetes in chemical treatment collections decreased 65% from the original to the fifth treatments. Apparently, substantial reductions in sea lamprey ammocoete populations occurred in these two streams.

Conversely, abundance of sea lamprey ammocoetes increased in some streams after successive chemical treatments. The factors responsible for these changes are not clearly understood. The reduction of native lampreys may have provided reestablished sea lamprey larvae with additional areas of suitable habitat. Collections from two other streams tributary to the north shore of Lake Michigan illustrate these changes (Table 3).

The Sturgeon and Ogontz rivers have a combined

TABLE 4. Number of recently metamorphosed sea lampreys captured by fyke nets during a 1-mo period in the fall in rivers of Lake Michigan, 1961–65 and 1978.

River	Year treated	1961	1962	1963	1964	1965	1978
Sturgeon	1963, 1966, 1970, 1974, 1977	215	330	25	37	42	0
Whitefish	1962, 1965, 1968, 1971, 1973, 1976, 1978	38	1	401	233	10	0
Ford	1964, 1967, 1971, 1972, 1974, 1976, 1977	410	78	58	17	2	0
Bark	1962, 1971, 1974, 1977	356	0	0	8	2	0
Cedar	1964, 1971, 1974, 1976	281	97	1	—	0	0
Total		1300	506	485	295	56	0

total length of 170 km (Brown 1944), and sea lamprey larvae were recovered from a major portion of this distance. They are regularly reinfected after successive chemical treatments, and year-classes are established annually.

The number of sea lamprey ammocoetes collected per hour from the Sturgeon and Ogontz rivers increased 80% from the first pretreatment surveys to the most recent stream surveys, but the number of native lamprey ammocoetes decreased 86%. Sea lampreys increased from 30% of all lamprey species before initial chemical treatments to 84% before the fourth treatments. Similarly, the percentage composition of sea lamprey ammocoetes in chemical treatment collections increased from 42 to 82%. Data examined for 63 streams tributary to the north and west shores of Lake Michigan revealed that these increases may be somewhat atypical. Abundance of sea lamprey ammocoetes has declined in 40, increased in 20, and changed little in 3.

Two streams tributary to the north shore of Lake Huron have also shown increases in the abundance of sea lamprey ammocoetes and substantial declines in the abundance of native lamprey ammocoetes after successive chemical treatments (Table 3).

The Pine and Carp rivers have a combined total length of 388 km (Brown 1944), and sea lamprey ammocoetes occupied a major portion of this distance. These streams are the largest tributaries to the north shore of Lake Huron in the United States, and collections demonstrated that they are also the greatest producers of sea lamprey ammocoetes in this area.

The number of sea lamprey ammocoetes collected per hour from the Pine and Carp rivers increased 56% from the first pretreatment surveys to the most recent stream surveys, whereas the number of native lamprey ammocoetes declined 87%. Sea lamprey larvae increased from 22% of all lamprey species before the initial treatments to 79% before the fourth treatments. Similarly, the percentage composition of sea lamprey ammocoetes in chemical treatment collections increased from 35 to 74 from the first to the fourth treatments.

Apparently, the abundance of sea lamprey ammocoetes has increased in these streams after successive chemical treatments, perhaps because of reduced density of native lampreys. Further, most reduced populations of adult sea lampreys may now be more selective during their spawning migrations as evidenced by lesser numbers of streams that are regularly reinfected. This example of increased abundance is atypical also, as an examination of all available data for 21 United States streams tributary to the north shore of Lake Huron revealed that abundance of sea lamprey ammocoetes has declined in 15% and increased in 6%.

TRANSFORMED INDIVIDUALS

Smith (1971) described a reduction in the numbers of recently metamorphosed sea lampreys migrating to Lake Superior after successive chemical treatments. Fyke nets fished in eight tributaries captured 72 young parasitic-phase lampreys in 1961, the number declined to 4 in 1965, and increased to 14 in 1966. However, nets fished for a 1-mo period on five south shore tributaries in late fall of 1978 still captured five transformed sea lampreys indicating that chemical treatments have not been totally effective in the elimination of these individuals.

Fyke nets were also fished in several streams tributary to the north and west shores of Lake Michigan (Table 4). Nets were fished from 1961 to 1965 and again in 1978. They were fished for about 1 mo in late fall 1978, and the catch for previous years was compared for the same period. The total number of young parasitic sea lampreys declined rapidly from 1300 in 1961 to 56 in 1965 and none in 1978. A substantial reduction was also noted in the catch from a fyke net set in the Ocqueoc River, a Lake Huron tributary (Great Lakes Fishery Commission 1973). The catch declined 91.5% from 3374 (average annual catch before treatment) to 296 (average annual catch after treatment).

Hodges (1972) showed a marked decline in total number of transformed sea lampreys after the first treatment of the Pere Marquette River, a major tributary to the east shore of Lake Michigan. The collections from a catch basket at a water-intake structure declined

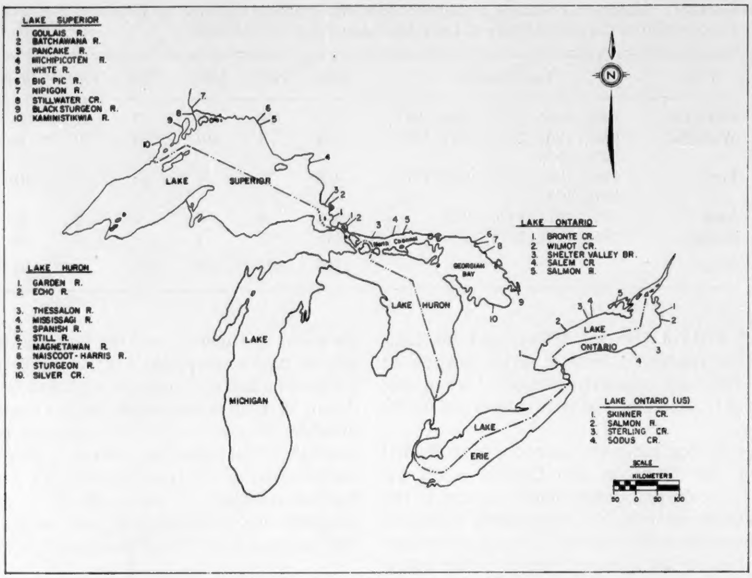
LAKE SUPERIOR
1 GOULAIS R.
2 BATCHAWANA R.
3 PANCAKE R.
4 MICHIPICOTEN R.
5 WHITE R.
6 BIG PIC R.
7 NIPIGON R.
8 STILLWATER CR.
9 BLACK STURGEON R.
10 KAMINISTIKWIA R.
LAKE HURON
1. GARDEN R.
2. ECHO R.
3. THESSALON R.
4. MISSISSAGI R.
5. SPANISH R.
6. STILL R.
7. MAGNETAWAN R.
8. NAISCOOT-HARRIS R.
9. STURGEON R.
10. SILVER CR.
LAKE ONTARIO
1. BRONTE CR.
2. WILMOT CR.
3. SHELTER VALLEY BR.
4. SALEM CR.
5. SALMON R.
LAKE ONTARIO (US)
1. SKINNER CR.
2. SALMON R.
3. STERLING CR.
4. SODUS CR.
LAKE SUPERIOR
LAKE MICHIGAN
LAKE HURON
GEORGIAN BAY
North Channel
LAKE ERIE
LAKE ONTARIO
N
SCALE
KILOMETERS
50 0 50 100

FIG. 2. Location of Great Lakes streams in which sea lampreys were collected to determine sex composition.

99.5% from 13 913 to 76 (average annual catches before and after treatment, respectively).

Effects of Lampricide Treatments on Growth

Hardisty (1944) reported different growth rates within streams for the European brook lamprey (*Lampetra planeri*). Growth of sea lamprey ammocoetes also varies considerably from stream to stream and within streams (Manion and McLain 1971; Purvis 1979). Although the factors that influence growth of ammocoetes are complex and interrelated, some important ones are density, temperature, stream size, and bottom type.

Purvis (1979) demonstrated that ammocoetes of year-classes established after a chemical treatment grow at a significantly faster rate than those of succeeding year-classes, and that under the influence of increasing density, the growth of each year-class is usually slower than that of all year-classes that preceded it. The increased density that results from the recruitment of successive year-classes probably depresses the growth rate of all year-classes and may serve as a self-regulating mechanism relative to the length attained.

Increased growth of transformed sea lampreys has also been reported. A gradual increase in length of newly transformed downstream migrants was reported for the Carp Lake River during a period when the spawning runs were blocked (Applegate 1961). Hodges (1972) demonstrated that the average annual length of recently metamorphosed sea lampreys increased from 134–142 mm before treatment with TFM to 153–164 mm in the migratory seasons after treatment.

Collections from chemical treatments of all Lake Michigan tributaries revealed that mean lengths of transformed sea lampreys increased from 143 mm during first treatments to 157 mm during second-round treatments. Purvis (1979) also reported an increase in length for transformed sea lampreys under such circumstances. Mean lengths increased in six streams tributary to the south shore of Lake Superior, from 140 mm during initial treatments to 166 mm in later treatments.

Effects of Lampricide Treatments on Sex Composition

Streams for sex ratio analysis were selected to provide representative samples of larvae and transformed individuals during initial and subsequent lampricide treatments and to represent a broad spectrum geographically within the Great Lakes (Fig. 2). Selected streams had divergent physical and chemical characteristics (discharge, gradient, temperature regime, water chemistry, and substrate composition); however, for sex ratio comparisons no attempt was made to group streams with similar characteristics.

Although sequential samples of larvae were available for most of the streams, scheduling of treatments did not always allow for continuous collections of metamorphosing specimens on every watershed, and consequently, because of the longer time interval after the 1961 treatments, detailed information on sex ratios of these individuals is limited to Lake Huron tributaries. Specimens examined were collected randomly throughout the stream during treatment with selective lampricides.

Adequate samples of lampreys from original lampricide treatments were only available for streams treated by the Canadian agent for sea lamprey control, and consequently, sex ratio analyses are limited to Canadian tributaries of lakes Superior and Huron and to the United States and Canadian tributaries of Lake Ontario.

No attempt has been made in this study to determine if the sexes are segregated geographically within a watershed; however, sex ratios appear to be variable within a stream, and establishment of a sex ratio from a one-station sample could be erroneous. Most samples were taken randomly from a wide range of stations within a watershed in an attempt to minimize any possible bias introduced by geographic segregation of sexes as reported by Lowe (1972) and Purvis (1979).

LAKE SUPERIOR

The data presented in Table 5 for nine Lake Superior streams indicate that sex compositions of the larvae were highly variable during the initial lampricide treatments conducted in 1958–63. The percentage of male larvae was highest (72) on the Michipicoten River and lowest (9) on the Nipigon River. Grouped geographically, the east shore tributaries had a significantly higher number of males (57%) in the original population than did the north shore watersheds with 20% males (χ^2 test, $P < 0.001$).

The percentage males collected during subsequent retreatments conducted on east shore tributaries between 1962 and 1977 decreased significantly to 28 (χ^2 test, $P < 0.001$), whereas the percentage males in north shore retreatments (1966–78) remained relatively unchanged at 22.

Although the percentage males decreased from 67 in 1959 (original treatment) to 55 in 1977 (11th treatment) on the Batchawana River, the shift in sex ratio was not as pronounced as that observed on the Pancake and Michipicoten rivers. The paucity of larvae collected during retreatments of the Batchawana River (1960–76) did not allow for examination of sex composition, and the present sex ratio may not be accurately represented by the 1977 sample, which was collected from a single station. The sex composition of 119 larvae collected from the delta of the Batchawana River during a treatment with Bayer 73 granules in 1978 was 22% males.

LAKE HURON

Information on the sex composition of populations of sea lampreys in Lake Huron tributaries is more complete than Lake Superior data in that representative samples of larvae and metamorphosed individuals were collected on several streams in sequential lampricide treatments (Table 5). As observed in the Lake Superior rivers, sex ratios of larvae and metamorphosed individuals were highly variable in Lake Huron streams during original treatments conducted in 1960–68. The Garden River exhibited a preponderance of males in the larval and metamorphosing stages with 70 and 85% males, respectively. In contrast, the sex ratio of the Sturgeon River was only 8 and 20% males, respectively. There was a definite segregation of males with regard to predominance of females relative to geographic location in Lake Huron, i.e. the predominately male streams were situated in the North Channel area, whereas a definite but variable excess of females was observed in Georgian Bay streams.

There was a highly significant lakewide shift towards increased femaleness in larvae examined from the second round of lampricide treatments on Lake Huron (χ^2 test, $P < 0.001$); however, the magnitude of the shift was variable between geographic locations within the lake, and was most dramatic in the predominately male North Channel streams. Sex composition of larvae remained relatively stable between second and third treatments at ~25% males on North Channel streams and 22% males on Georgian Bay tributaries. The change in sex ratio to increased femaleness between first and second treatments also was apparent in the transformed populations in North Channel streams (χ^2 test, $P < 0.001$); however, the sex ratio of Georgian Bay metamorphosed individuals remained virtually unchanged at 32% males.

LAKE ONTARIO

Sex ratios of larvae collected during the initial lampricide treatments in 1971–72 on nine Lake Ontario streams were less variable than those from original lakes Superior and Huron treatments (Table 5). The highest and lowest percentage of males (54 and 13) were observed on Skinner and Sodus creeks, both tributary to United States waters of Lake Ontario. There was also an apparent scarcity of predominately male streams when compared with lakes Superior and Huron.

Although significant changes in sex ratios occurred in individual streams tributary to the north shore of Lake Ontario, there was no definite trend to increased femaleness, whereas two south shore tributaries (Salmon River and Skinner Creek) demonstrated statistically significant changes in the sex composition to increased femaleness. The shift from 27% males in 1972 to 19% in 1975 in Sterling Creek was not significant. Collectively, the north shore streams experienced a significant shift in sex ratio to increased maleness between first and second treatments, whereas south shore watersheds shifted to increased femaleness between first and subsequent treatments. The sex composition of larvae

TABLE 5. Number and percentage males by treatment sequence in samples of larval and transformed sea lampreys collected during lampricide treatments on selected tributaries to Lakes Superior, Huron, and Ontario.

Lake and stream	Larvae	Transformed
	Number in sample (treatment sequence) % males	Number in sample (treatment sequence) % males
Superior		
East Shore		
Goulais	141 (1) 46, 108 (2) 57, 142 (3) 37, 163 (5) 36, 106 (6) 28	63 (2) 54, 39 (5) 23
Batchawana	60 (1), 67, 29 (11) 55	20 (1) 65
Pancake	84 (1) 52, 61 (4) 15, 36 (5) 14, 18 (6) 17	
Michipicoten	81 (1) 72, 139 (2) 19, 152 (4) 18, 127 (5) 15	
Total	366 (1) 57	
North Shore		
White	180 (1) 28, 27 (4) 26	45 (1) 33
Big Pic	70 (1) 30, 121 (3) 26	64 (3) 19
Nipigon	256 (1) 9, 32 (2) 14, 95 (a) 13	28 (a) 14
Black Sturgeon	22 (1) 23, 205 (2) 11	61 (2) 13
Kaministikwia	102 (1) 27, 123 (4) 30, 142 (5) 39, 112 (6) 23	34 (4) 68, 10 (6) 50
Total	630 (1) 20	
Huron		
North Shore		
Garden	416 (1) 70, 45 (2) 7, 299 (3) 21	473 (1) 85, 26 (2) 31, 42 (3) 26
Echo	733 (1) 65, 325 (2) 36, 189 (3) 19	1173 (1) 70
Thessalon	906 (1) 38, 133 (2) 28, 274 (3) 30	417 (1) 40 52 (3) 67
Mississagi	287 (1) 46, 513 (2) 20	285 (1) 69, 210 (2) 38
Spanish	101 (1) 51, 38 (2) 37	242 (1) 50
Total	2443 (1) 53, 1054 (2) 26, 762 (3) 24	2590 (1) 66, 236 (2) 37, 94 (3) 49
Georgian Bay		
Still	158 (1) 25, 455 (2) 23	287 (1) 41, 675 (2) 31
Magnetawan	122 (1) 41, 165 (2) 36, 24 (3) 30	43 (1) 35, 27 (2) 37
Naiscoot	64 (1) 48, 281 (2) 37, 110 (3) 44	69 (1) 39, 1060 (2) 43
Sturgeon	240 (1) 8, 658 (2) 12, 356 (3) 8	64 (1) 20
Silver	180 (1) 39, 384 (2) 24, 176 (3) 21	
Total	764 (1) 27, 1943 (2) 22, 666 (3) 22	463 (1) 37, 1762 (2) 38
Ontario		
Canada		
Bronte	693 (1) 39, 181 (2) 40, 82 (3) 42	
Wilmot	263 (1) 26, 22 (2) 36, 35 (3) 29	
Shelter Valley	154 (1) 26, 141 (2) 41, 61 (3) 39	
Salem	16 (1) 50, 163 (2) 39	
Salmon	55 (1) 53, 250 (2) 55, 18 (3) 56	
Total	1181 (1) 40, 757 (2) 44, 196 (3) 40	
United States		
Skinner	246 (1) 54, 117 (2) 40	
Salmon	810 (1) 49, 239 (3) 31	
Sterling	73 (1) 27, 175 (2) 19	
Sodus	164 (1) 13, 67 (2) 30	
Total	1293 (1) 48, 598 ( ) 29	

[a] Specimens collected in a survey.

collected during third treatments on north shore streams changed slightly towards femaleness and was nearly equal to the sex ratio observed during first treatments. The most pronounced shift in sex ratios in Lake Ontario occurred in south shore tributaries and has been to increased femaleness.

ESTABLISHMENT OF SEX COMPOSITION

Limited information on the sex compositions of larval sea lampreys and downstream migrants has been presented by Hardisty (1960), Applegate and Thomas (1965), and Purvis (1979). Hardisty determined that the sex ratio of larvae collected from the Ocqueoc River was about equal. Applegate and Thomas (1965) examined the sex of recently transformed downstream migrants from the Ocqueoc River and three Lake Michigan tributaries: Carp Lake, Ogontz, and Pere Marquette rivers, and concluded that "populations of recently transformed sea lampreys in the Great Lakes are normally characterized by a small but variable preponderance of females" and that the disproportionate number of males (76%) observed in the 1960–61 run of downstream migrants on Carp Lake River was "atypical of the sex composition of recently transformed sea lamprey populations in Great Lakes streams." Purvis (1979) indicated that a preponderance of males existed in transforming populations of sea lampreys present in a number of streams tributary to Lakes Superior, Huron, and Michigan before and during initial lampricide treatments, and that sex ratios of larvae and transformed individuals collected from subsequent lampricide treatments of these same streams had shifted to disproportionate femaleness.

The information presented in this report indicates that, historically, highly variable sex ratios existed in sea lamprey ammocoetes and transformed populations dwelling in Great Lakes tributaries and that with the advent of chemical control a significant shift to increased femaleness has occurred in some streams.

Although much attention has been given to the factors regulating sexual differentiation in lower vertebrates, factors influencing the sexual determination in sea lamprey larvae are still in doubt. Hardisty (1965) acknowledges the views held by other authors that sex in the lower vertebrates may be determined phenotypically and could possibly be influenced by such environmental factors as temperature and density. He believed such factors might explain atypical sex ratios in larval lampreys. However, he found that sex ratios in larval populations of *Lampetra planeri* and the sea lamprey did not differ significantly, but approached 1:1 in streams with divergent characteristics. This led him to believe that environmental factors do not have any decisive influence on the sex differentiation of the ammocoete. In the Great Lakes, however, the highly variable sex ratios of larval sea lamprey populations present in streams with divergent physical and chemical characteristics lend credibility to the view that environmental factors may play an important role in sexual differentiation of the ammocoete.

Although this report does not produce affirmative evidence to suggest that temperature influences the sex determination of sea lamprey ammocoetes, samples of larvae used in establishing the widely disparate sex ratios originated from streams with divergent temperature regimes. Among Lake Superior tributaries, the Nipigon River probably has the coldest and least variable temperature regime, whereas on Lake Huron, the Sturgeon River has relatively cold water temperatures. The percentage of males in both streams (20 and 10) was extremely low (Table 5) and possibly cold water might favor sexual differentiation towards females.

More substantial evidence can be presented to support the views that sex differentiation in sea lamprey larvae is density dependent (Purvis 1979). When original treatments were conducted on tributaries referred to in this report, the predominately male streams all exhibited one common characteristic — high densities of larvae per unit area of habitat. Conceivably, high density could induce stress through crowding and influence sexual differentiation of larvae, presumably toward maleness. Crowding could also cause a disproportionate amount of female mortality after sexual differentiation has been completed.

The most pronounced shifts in sex ratios of sea lamprey larvae and transforming populations have been towards increased femaleness and occurred predominately on high density streams supporting disproportionate numbers of males during original treatments. Possibly reduction by repetitive lampricide treatments of density-dependent factors has resulted in a shift to femaleness in reestablished populations of ammocoetes. Sex compositions on streams where relatively low densities of larvae existed during original treatments remained remarkably stable since the advent of chemical control.

The Salmon River, a tributary to Canadian waters of Lake Ontario, often exhibits very low summer discharge over limestone and clay substrates and experiences relatively high water temperatures. Populations of sea lamprey larvae reestablished between lampricide treatments tend to be relatively dense and reside in marginal habitat. The fact that the sex composition has remained predominately male after three successive treatments (Table 5) suggests that environmental factors such as high temperature and/or density may be influencing sexual differentiation towards maleness in this stream.

Various workers have indicated that an age-dependent differential transformation rate exists for the sexes of sea lamprey ammocoete populations. Applegate and Thomas (1965) concluded from a study of the sex composition of recently transformed migrants in Carp Lake River that sea lamprey females transform at an earlier age than do the males.

Purvis (1970) in a study on the northern brook lamprey (*Ichthyomyzon fossor*) in the Sturgeon River, a southern Lake Superior tributary, provided evidence to suggest that male northern brook lampreys begin transformation at an earlier age. More conclusive evidence that sea lamprey males transform first has been presented by Manion and Smith (1978) and Purvis (1979). When transformation of a single isolated year-class of sea lampreys in the Big Garlic River began in 1966, the sex ratio of downstream migrants was 51% males; however, the sex ratio of the larval population for the same year was 21% males. From 1966 to 1972 the percentage of male-transformed individuals declined steadily and was 15 in 1972, whereas the sex ratio of ammocoetes remained nearly stable at 20% males. Examples of earlier transformation in males are illustrated in Table 5.

Between 1960 and 1977 the sex composition of larval sea lampreys in the Kaministikwia River, a Lake Superior tributary, was predominately female. However, small samples of transformed individuals collected

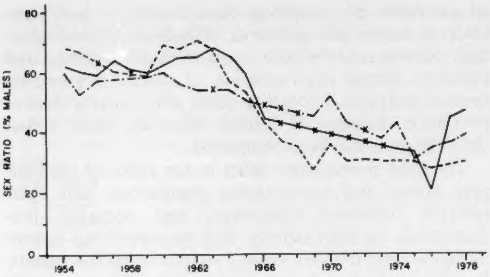

FIG. 3. Percentage males of adult sea lampreys collected from index streams on Lakes Superior (broken line), Michigan (solid line), and Huron (dots and broken line), 1954–78. An x indicates no collection.

in 1969 and 1977 were 68 and 50% males, respectively. In the Thessalon River, a Lake Huron tributary, the sex ratio of larvae in 1975 was 30% males, whereas 67% of 52 transformed individuals were males.

The most comprehensive data of sex composition of larvae and transformed individuals were collected from first and second lampricide treatments on Lake Huron tributaries (Table 5). Collectively, for transformed individuals, the percentage males present was significantly higher than in the larval populations (χ^2 test, $P < 0.001$).

For most populations sampled, equality of sexes in larval and metamorphosed stages was not observed. Hardisty (1960) concluded "that the female suffers a much higher mortality than the male at some stage in the life cycle between metamorphosis and spawning" and "that the factors which are responsible for this increased female mortality must operate with varying intensity at different times and in different localities." The fact that for most streams significant differences existed between sex ratios of larval and transformed individuals from the same watershed during original treatments indeed suggests the possibility of differential mortality of the female at the critical period of metamorphosis.

Different annual recruitment rates to larval populations with differential mortality and transformation of the sexes may have contributed to the highly variable sex ratios observed in larval and metamorphosed stages.

CHANGE IN ADULT SEX RATIOS

Control of the sea lamprey through treatment of tributary streams with selective lampricides was instrumental in decreasing the numbers of parasitic adults (Smith 1971). The decline, as indicated by a reduction of spawning-phase adults collected at electrical barriers and mechanical weirs, was accompanied by a pronounced shift in the sex ratio (Fig. 3). During peak years of lamprey abundance, spawning runs were characterized by a preponderance of males, but as the magnitude of the runs decreased, the percentage of males

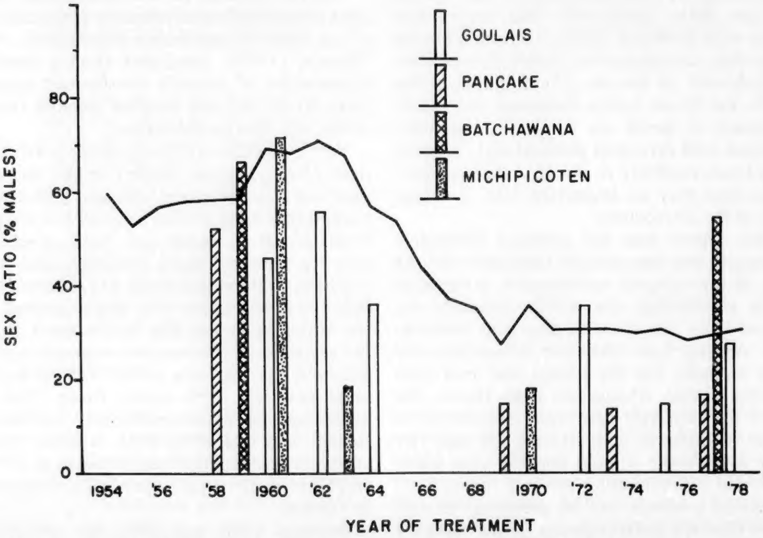

FIG. 4. Percentage males of adult sea lampreys (line) collected from index streams of Lake Superior, 1954–78, and of larval sea lampreys (bars) collected from four east shore Lake Superior streams during lampricide treatments, 1958–78.

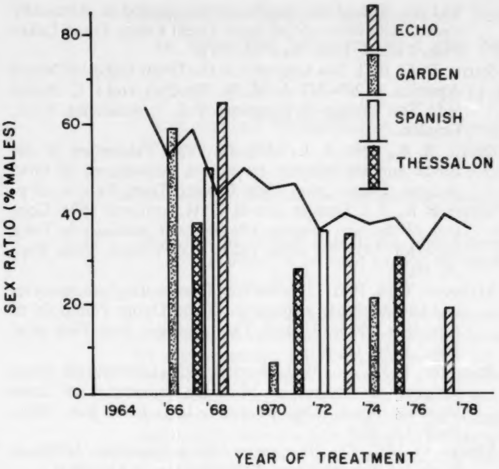

FIG. 5. Percentage males of adult sea lampreys (line) collected from five electrical barriers on tributaries of the North Channel, Lake Huron, 1965–78, and of larval sea lampreys (bars) collected from four North Channel tributaries during lampricide treatments, 1966–77.

also decreased accordingly. Smith (1971) found that a positive correlation existed between abundance and the percentage males in Lakes Superior and Huron. This phenomenon was also recorded by Hardisty (1961) in spawning populations of *Lampetra planeri* in the River Yeo in England.

Smith (1971) considered the shift in sex composition towards males in an increasing sea lamprey population and to females in a decreasing population to be a natural means of population control. The decline in the numbers of adults paralleled by a decrease in percentage of males collected in the Ocqueoc River before the advent of chemical control in 1960 lends credibility to the "natural population control" hypothesis; however, similar decreases in numbers and shifts in sex ratios did not occur in Lakes Superior and Michigan until after the initiation of lampricide treatments in 1958 and 1960, respectively.

The shift to a predominance of females in the adult populations of sea lampreys in the upper Great Lakes apparently has been precipitated by a similar shift in the larval and metamorphosed stages of the life cycle (Fig. 4 and 5). Presumably the disproportionate number of adult females observed in the upper Great Lakes resulted from destruction of dense larval populations that were predominately male at the onset of chemical control. Reestablishment of highly female larval populations occurred in the once predominately male streams, and larvae not eradicated by subsequent retreatment of these predominately female streams are contributing to adult populations in the upper lakes.

Although the sex compositions of larval populations dwelling in streams tributary to the north shore of Lake Ontario have not changed significantly, a shift in the sex ratio to increased femaleness occurred in three south shore tributaries — Salmon River and Skinner and Sterling creeks (Table 5). The predominance of males observed in some upper Great Lakes tributaries, and consequently, any changes to increased femaleness in the adult sea lamprey population may be more subtle than observed on the upper lakes. Sex ratio data for Lake Ontario adults, though limited, have been collected continuously since 1968 from the Humber River, a north shore tributary. Sex composition of the adult spawning runs examined between 1968 and 1977 was predominately male (50 to 58%); however, in 1978 the percentage of males dropped to 42. Obviously, any conclusions relative to a lakewide sex ratio shift would be premature at this time, but the decline in the percentage males collected at the Humber River in 1978 may be evidence that a trend towards increased femaleness in adult sea lampreys, similar to that observed in the upper Great Lakes, may be occurring in Lake Ontario.

Acknowledgments

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APPLEGATE, V. C. 1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 55: 237 p.

1961. Downstream movement of lampreys and fishes in the Carp Lake River, Michigan. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 387: 71 p.

APPLEGATE, V. C., J. H. HOWELL, J. W. MOFFETT, B. G. H. JOHNSON, AND M. A. SMITH. 1961. Use of 3-trifluoromethyl-4-nitrophenol as a selective sea lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 1: 35 p.

APPLEGATE, V. C., J. H. HOWELL, AND M. A. SMITH. 1958. Use of mononitrophenols containing halogens as selective sea lamprey larvicides. Science 127(3294): 336–338.

APPLEGATE, V. C., AND M. L. H. THOMAS. 1965. Sex ratios and sexual dimorphism among recently transformed sea lampreys, *Petromyzon marinus* Linnaeus. J. Fish. Res. Board Can. 22: 695–711.

BRAEM, R. A., AND W. J. EBEL. 1961. A back-pack shocker for collecting lamprey ammocetes. Prog. Fish Cult. 23: 87–91.

BROWN, C. J. D. 1944. Michigan streams — their lengths, distribution, and drainage area. Mich. Dept. Conserv. Inst. Fish. Res. Misc. Publ. 1: 21 p.

GREAT LAKES FISHERY COMMISSION. 1958, 1960, 1961, 1971, 1973. Annual Reports.

HANSEN, M. J., AND D. W. HAYNE. 1962. Sea lamprey larvae in Ogontz Bay and Ogontz River, Michigan. J. Wildl. Manage. 26 (3): 237–247.

HARDISTY, M. W. 1944. The life history and growth of the brook lamprey (*Lampetra planeri*). J. Anim. Ecol. 13: 110–122.

1960. Sex ratio of ammocetes. Nature (London) 186: 988–989.

1961. Sex composition of lamprey populations. Nature (London) 191: 1116–1117.

1965. Sex differentiation and gonadogenesis in lampreys. Part II. J. Zool. 146: 346–387.

HODGES, J. W. 1972. Downstream migration of recently transformed sea lampreys before and after treatment of a Lake Michigan tributary with a lampricide. J. Fish. Res. Board Can. 29: 1237–1240.

HOWELL, J. H., E. L. KING JR., A. J. SMITH, AND L. H. HANSON. 1964. Synergism of 5,2′-dichloro-4′-nitrosalicylanilide and 3-trifluoromethyl-4-nitrophenol in a selective lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 8: 21 p.

LOWE, D. R. 1972. Variations in body composition of preadult landlocked sea lamprey, *Petromyzon marinus* L. in relation to size and season. M.S. thesis, Univ. of Guelph, Guelph, Ont. 81 p.

MANION, P. J., AND A. L. MCLAIN. 1971. Biology of larval sea lampreys (*Petromyzon marinus*) of the 1960 year class, isolated in the Big Garlic River, Michigan, 1960–65. Great Lakes Fish. Comm. Tech. Rep. 16: 35 p.

MANION, P. J., AND B. R. SMITH. 1978. Biology of larval and metamorphosing sea lampreys, *Petromyzon marinus*, of the 1960 year class in the Big Garlic River, Michigan, Part II, 1966–72. Great Lakes Fish. Comm. Tech. Rep. 30: 35 p.

PRATT, V. S. 1952. A measure of the efficiency of alternating and direct current fish shockers. Trans. Am. Fish. Soc. 81: 63–68.

PURVIS, H. A. 1970. Growth, age at metamorphosis, and sex ratio of northern brook lamprey in a tributary of southern Lake Superior. Copeia 1970: 326–332.

1979. Variations in growth, age at transformation, and sex ratio of sea lampreys reestablished in chemically treated tributaries of the upper Great Lakes. Great Lakes Fish. Comm. Tech. Rep. 35: 36 p.

SMITH, B. R. 1971. Sea lampreys in the Great Lakes of North America, p. 207–247. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London.

SMITH, B. R., AND A. L. MCLAIN. 1962. Estimation of the brook and sea lamprey ammocete populations of three streams. Great Lakes Fish. Comm. Tech. Rep. 4: 18 p.

SMITH, B. R., J. J. TIBBLES, AND B. G. H. JOHNSON. 1974. Control of the sea lamprey (*Petromyzon marinus*) in Lake Superior, 1953–70. Great Lakes Fish. Comm. Tech. Rep. 26: 60 p.

STAUFFER, T. M. 1961. Distribution of sea lamprey ammocoetes in Lake Michigan tributaries of the Upper Peninsula of Michigan, 1955–59. Mich. Dep. Conserv. Inst. Fish. Res. Misc. Publ. 14: 21 p.

STAUFFER, T. M., AND M. J. HANSEN. 1958. Distribution of sea lamprey ammocetes in Michigan tributaries of Lake Superior. Mich. Dep. Conserv. Inst. Fish. Res. Misc. Publ. 11: 25 p.

STERBA, G. 1962. Die Neunaugen (*Petromyzonidae*). *In* Handbuch der Binnerfischerei Mitteleuropas 3(X): 138 p.

TIBBLES, J. J. 1959. Preparations for lamprey control in Lake Huron. Progr. Rep. Fish. Res. Board Can. 1: 38 p.

VLADYKOV, V. D. 1960. Description of young ammocoetes belonging to two species of lampreys: *Petromyzon marinus* and *Entosphenus lamotteni*. J. Fish. Res. Board Can. 17: 267–288.

Changes in Spawning Runs of Sea Lamprey (*Petromyzon marinus*) in Selected Streams of Lake Superior after Chemical Control[1]

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During lampricide treatment of a stream, sea lamprey, *Petromyzon marinus*, that will constitute the spawning run the following spring inhabit the Great Lakes and are not affected by the treatment. However, the number of adults captured at electrical barriers declined as much as 99% in some streams 1 year after chemical treatment. Large declines of adults were noted in streams which were treated late in the year. Streams in which significant populations of larval lampreys survived the chemical treatment, or contained lentic populations, continued to attract adults. Adult sea lampreys could be attracted to sea lamprey ammocoetes in streams or in offshore areas and hence use this as one of a number of clues to determine rivers suitable for spawning.

Key words: sea lamprey, olfaction, orientation/homing, spawning migration, habitat alteration (chemical), *Petromyzon marinus*, lampricides

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Au moment ou l'on traite un cours d'eau aux lampricides, les grandes lamproies marines, *Petromyzon marinus*, qui constitueront la montée reproductrice du printemps suivant se trouvent dans les Grands Lacs et ne sont pas affectées par le traitement. Cependant, le nombre des adultes capturés aux barrières électriques accuse des diminutions allant jusqu'à 99% dans certains cours d'eau 1 an après le treatement chimique. Dans les cours d'eau traités tard dans l'année, on note une diminution importante des adultes. Les cours d'eau dans lesquels des populations abondantes de lamproies larvaires ont survécu au traitement chimique, ou qui contiennent des populations lentiques, continuent à attirer les adultes. Il est possible que les adultes soient attirés par les ammocoètes de grande lamproie marine dans les cours d'eau ou les régions du large, et qu'elles utilisent cette attraction comme un des nombreux indices qui leur permet de choisir les rivières convenables pour la fraie.

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SEA lamprey (*Petromyzon marinus*) have been controlled successfully in the Great Lakes by using selective toxicants, 3-trifluoromethyl-4-nitrophenol (TFM) and 2′,5-dichloro-4′-nitrosalicylanilide (Bayer 73), to kill larval lampreys in streams (Applegate et al. 1961; Howell et al. 1964). The effect of chemical treatments in eight selected streams on the size of subsequent runs of spawning sea lampreys is examined in this paper. Information on the possible effects of the lampricides on the size of the spawning migrations of sea lampreys was obtained during the operation of electric barriers designed to capture lampreys on their spawning runs in these streams.

Factors that may influence the selection of streams for spawning by sea lampreys are also discussed. Based on the literature, it is apparent that little is known about the factors or processes used by sea lampreys in selecting a stream for spawning. Manipulation of the factors or processes used in stream selection could lead to new methods of controlling this parasite.

Materials and Methods

Catch records of spawning-run sea lampreys are available from electric barriers which were used in an attempt to control the parasite on the United States side of Lake Superior from 1953 to 1960 (McLain et al. 1965). After

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TABLE 1. Number of adult sea lamprey taken at electric barriers operating in eight tributaries of the south shore of Lake Superior through July 13, 1953–78. (An asterisk indicates the year of chemical treatment.)

Year	Betsy	Two Hearted	Sucker	Chocolay	Iron	Silver	Brule	Amnicon	Total
1953	221	371	750	—	—	—	—	—	1 342
1954	561	620	1299	1174	65	216	—	—	3 935
1955	567	587	1678	3350	183	765	—	—	7 130
1956	1553	1597	3856	6747	319	918	—	—	14 990
1957	774	7586	3506	8088	717	2757		11 038	38 435
1958	1071	3418	1727*	6168*	401*	2111*	22 593	7 584*	45 073
1959	1000	3990*	2457*	3490	257	773	19 225*	980	32 172
1960	686*	4222	4670	4167	310	1261	9 523	1 081	25 920
1961	1366	7498	3209*	4201*	2430	5052*	22 478	4 741	50 975
1962	316*	1757*	474	423	1161*	267	2 026*	879*	7 303
1963	444	2447	698*	358	110	760	3 418	131	8 366
1964	272	1425	386	445	178	593	6 718	232	10 249
1965	187*	1265*	532*	563	283	847	6 163*	700	10 540
1966	65	878	223	260*	491	1010*	226	938	4 091
1967	57	796	166*	65	643*	339	364	200*	2 630
1968	78	2132	658	122	82	1032	2 657	148	6 909
1969	120	1104	494*	142	556	1147*	3 374*	1 576	8 513
1970	87*	1132*	337	291*	713	321	167	1 733	4 781
1971	104	1035	485*	53	1518*	340	1 754	4 324*	9 613
1972	146	1507	642*	294	280*	2574*	4 121*	132*	9 696
1973	294	894*	468*	270*	16	495*	261	149	2 847
1974	201*	489	249*	17	1	117*	568*	270	1 912
1975	197	683*	478*	24	8	206*	285	2 606*	4 487
1976	148	229	314	10	33	199*	1 085	80	2 098
1977	162	654	533*	4	66	312*	2 572*	493	4 796
1978	185*	355	974	6	26*	162*	794	2 310	4 812

the 1960 season, the barriers (reduced in numbers from 45 to 29) served as monitoring devices to assess the effects of chemical control which was initiated in 1958 (Applegate et al. 1961). Budget restrictions, accompanied by expansion of the chemical control program, brought about further reductions to 26 barriers in 1963, 22 in 1964, and 16 in 1965. From 1966 to 1970, between 78 and 91% of sea lampreys captured were from 8 of the 16 barriers. In 1971, the number of assessment barriers operated on Lake Superior was reduced to these eight most productive barriers which are used as the basis for this study. Electric barriers were operated on Canadian tributaries of Lake Superior in a comparable manner to electric barriers in the United States. Operation of these barriers was discontinued in 1967 when it was evident that the data collected at the Canadian barriers indicated the same trends and changes as shown by catches from barriers in the United States (Smith et al. 1974).

Catch data from the eight streams along the south shore of Lake Superior are available annually from 1958 to 1978, with records from as early as 1953 for some rivers (Table 1, Fig. 1). All of the streams have unique characteristics which contributed to their ability to attract adult sea lampreys. Beginning in 1971, these eight streams were included in an intensified control program, or were chemically treated as often as necessary; consequently, intervals of time between treatments varied (Smith and Tibbles 1980). Factors used to determine necessity of treatments are lentic populations of ammocoetes, growth rate and abundance of ammocoetes, presence of ammocoetes residual from previous chemical treatments, and number of adult sea lampreys using the stream.

Results

BETSY RIVER

The Betsy River empties into Whitefish Bay about 18 km north of the mouth of the Tahquamenon River, the largest stream tributary to Whitefish Bay. The Tahquamenon River averages 17 m^3/s, compared with an average of only 1.7 m^3/s in the Betsy River (Table 2). A concrete dam which is a barrier to upstream migration of fish and lampreys was constructed in 1965 about 13 km from the mouth of the Betsy River.

An electrical barrier has been operated on this river since 1953. Catches of sea lampreys at the barrier varied from a high of 1553 in 1956 to a low of 57 in 1967 (Table 1). The catch in 1974 was 10.5% of the entire number captured at the eight index barriers whereas in 1968 and 1971 the numbers captured contributed only 1.1% of the total annual catch for each year (Table 3).

Chemical treatments of the Betsy River had little or no effect on the number of migrant sea lampreys that entered this stream the year after treatment (Table 1). The percentage contribution to the index barrier catch increased after treatments in June 1960 and 1962, and July 1970, whereas after the August treatments in 1965 and 1974, spawning runs declined in numbers and in percentage contribution (Tables 3 and 4).

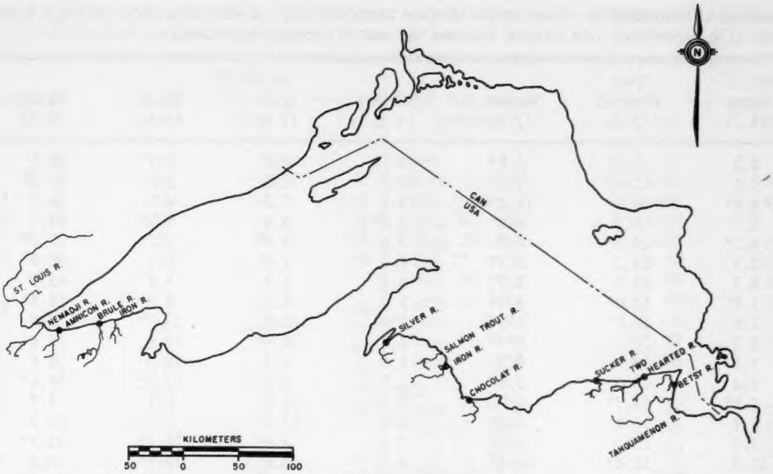

FIG. 1. Lake Superior, showing locations of streams where eight index barriers were operated (dots) and other tributaries discussed in the text.

The size of the spawning run in the Betsy River does not appear to be influenced by treatment of the Tahquamenon River which is over 10 times as large. The adult run into the Betsy River in 1961 increased in percentage contribution to the barrier catch and total numbers after treatment of both the Tahquamenon and Betsy rivers in 1960. The streams have not been treated the same year since 1960; however, treatment of the Tahquamenon River caused little or no appreciable change in the catch at the barrier on the Betsy River.

In the 15 years before intensification of control became effective in 1973, catches from the barrier on the Betsy River averaged 2.4% of the total catch, compared with an average of 6.6% in the 6 years after 1973. The reason the number of sea lampreys captured at the barrier contributed more to the total catch after intensification is unknown, although sea lampreys from areas where chemical control is impractical (St. Marys River) are suspected of contributing significant numbers of adults to the spawning run in the Betsy River.

TABLE 2. Physical features of rivers with electric barriers.

River	Kilometres of main stream	Kilometres of tributaries	Average flow at mouth (m^3/s)	Location of barrier above mouth (km)
Betsy	48	66	1.7	8.0
Two Hearted	64	110	5.7	0.3
Sucker	45	52	2.8	3.2
Chocolay	24	172	4.3	12.9
Iron	8	96	1.8	3.0
Silver	29	79	1.1	0.5
Brule	58	96	5.7	0.7
Amnicon	58	162	1.4	4.8

TWO HEARTED RIVER

The Two Hearted River is the first major river system along the shoreline of southern Lake Superior, west of Whitefish Bay. No sea lamprey ammocoete populations have been found off the mouth of the stream.

An electric barrier has been operated on the Two Hearted River since 1953. The largest catch of sea lampreys at the barrier was 7586 in 1957; the lowest was 229 taken in 1976 (Table 1). The percentage contribution to the total index barrier catch ranged from a high of 31.4% in 1973 to a low of 7.4% in 1978 (Table 3). The number of sea lampreys captured and the percentage contribution to the total index barrier catch increased the year after the first two treatments in June 1959 and 1962. The second largest catch recorded at this barrier was 2 years after the first treatment.

Treatments of the Two Hearted River in July of 1965, 1970, 1973, and 1975 resulted in a decline in the percentage contribution to the total index barrier catch the following year, except in 1965 when the percentage contribution increased from 12 to 21.5 (Table 3). Actual numbers captured in 1965 were 1265, whereas only 878 were captured in 1966. The catch from all eight barriers also declined from 10 540 in 1965 to 4091 in 1966.

Young-of-the-year sea lamprey ammocoetes probably survived the treatment of the Two Hearted River since treatments were completed before the end of the spawning season or during the stages of development

TABLE 3. Percentage contribution by stream to sea lamprey catch, by year, on the south shore of Lake Superior, 1958–78. Average flow (m³/s) in parentheses. (An asterisk indicates the year of chemical treatment.)

Year	Betsy (1.7)	Two Hearted (5.7)	Sucker (2.8)	Chocolay (4.3)	Iron (1.8)	Silver (1.1)	Brule (5.7)	Amnicon (1.4)
1958	2.3	7.6	3.8*	13.7*	0.9*	4.7*	50.1	16.8*
1959	3.1	12.4*	7.6*	10.8	0.8	2.4	59.8*	3.0
1960	2.6*	16.3	18.0	16.1	1.2	4.9	36.7	4.2
1961	2.7	14.7	6.3*	8.2*	4.8	9.9*	44.1	9.3
1962	4.3*	24.1*	6.5	5.8	15.9*	3.7	27.7*	12.0*
1963	5.3	29.2	8.3*	4.3	1.3	9.1	40.9	1.6
1964	2.7	13.9	3.8	4.3	1.7	5.8	65.5	2.3
1965	1.8*	12.0*	5.0*	5.3	2.7	8.0	58.5*	6.6
1966	1.6	21.5	5.5	6.4*	12.0	24.7*	5.5	22.9
1967	2.2	30.3	6.3*	2.5	24.4*	12.9	13.8	7.6*
1968	1.1	30.9	9.5	1.8	1.2	14.9	38.5	2.1
1969	1.4	13.0	5.8*	1.7	6.5	13.5*	39.6*	18.5
1970	1.8*	23.7*	7.0	6.1*	14.9	6.7	3.5	36.2
1971	1.1	10.8	5.0*	0.6	15.8*	3.5	18.2	45.0*
1972	1.5	15.5	6.6*	3.0	2.9*	26.5*	42.5*	1.4*
1973	10.3	31.4*	16.4*	9.5*	0.6	17.4*	9.2	5.2
1974	10.5*	25.6	13.0*	0.9	0.1	6.1*	29.7*	14.1
1975	4.4	15.2*	10.7*	0.5	0.2	4.6*	6.4	58.1*
1976	7.1	10.9	15.0	0.5	1.6	9.5*	51.7	3.8
1977	3.4	13.6	11.1*	0.1	1.4	6.5*	53.6*	10.3
1978	3.8*	7.4	20.3	0.1	0.5*	3.4*	16.5	48.0*

when the embryos were resistant to the chemical (Piavis and Howell 1975).

SUCKER RIVER

Until 1973 the Sucker River flowed into East Bay, a 31-ha lentic environment, through a 0.8-km channel into West Bay, then emptied into Lake Superior. The sandspit that separated East Bay from Lake Superior was destroyed in 1973, and now the river flows directly into the lake. East Bay contained an estimated 96 000 sea lamprey ammocoetes (Wagner and Stauffer 1962), which were killed in 1961 when East Bay was treated with toxaphene (Gaylord and Smith 1966), a general toxicant that destroyed the entire fish population.

Since 1961 the Sucker River has been treated with lampricides annually or semiannually to destroy the young-of-the-year larvae before they wash or drift into the lentic environment off the mouth (Table 3). Treatment with TFM had little effect on the number of adults that migrated into the river since the toxaphene treatment in 1961. The number of migrants fluctuated from a low of 166 in 1967 to a high of 974 in 1978, the largest run to use the stream since 1961 when 3209 adults were captured at the barrier (Table 1).

In 1961 the Sucker River accounted for 6.3% of the barrier catch, compared with 20.3% in 1978 (Table 3). The factors that may have influenced this increase are not clearly understood. The physical changes that accompanied the destruction in 1973 of the sandspit that formed East and West bays could provide more attraction to adults seeking a stream during the spawning migration.

CHOCOLAY RIVER

Mechanical or electric barriers were operated on the Chocolay River from 1951 to 1978. In 1957, 8088 sea lampreys, the largest run to enter the river, were captured at the barrier (Table 1). (No known lentic populations are associated with the stream.) On Lake Superior, only the barriers on the Amnicon and Brule rivers captured more sea lampreys in one season. In 1960 the Chocolay River contributed 16.1% of the total index barrier catch (Table 3).

The decline in the number of adult sea lampreys migrating into the Chocolay River was dramatic. The count of adult migrants at the barrier declined the year after each treatment (Table 4). No known reproduction occurred in the Chocolay River upstream from the barrier since 1973. Total destruction of the ammocoete population was believed to have occurred during the 1973 treatment and was accompanied by a continued decline in the number of adults migrating into the stream. Since 1973 the Chocolay River catch contributed less than 1% of the total Lake Superior barrier catch (Table 3). A combination of chemical treatments and operation of the electric barrier prevented successful spawning in the upper river after 1973. However, a small number of adults are still attracted to the Chocolay River each year and small populations of sea lamprey ammocoetes become reestablished in the lower river.

IRON RIVER

The barrier on the Iron River contributed a high

TABLE 4. Percentage change in the sea lamprey catch at the eight electric barriers on the south shore of Lake Superior from the total taken the year of chemical treatment to the total 1, 2, and 3 yr later.

River and date of treatment	% change		
	1 yr	2 yr	3 yr
Betsy			
June 1, 1960	94	−55	−37
June 26, 1962	41	−14	−41
Aug. 27, 1965	−65	−70	−58
July 23, 1970	20	68	238
Aug. 22, 1974	−2	−26	−19
Two Hearted			
June 15, 1959	6	87	−56
June 12, 1962	39	−19	−28
July 30, 1965	−31	−37	−69
July 12, 1970	−9	33	−21
July 15, 1973	−45	−24	−74
July 26, 1975	−64	−4	−48
Sucker			
Oct. 10, 1958	42	170	85
Aug. 4, 1959	90	31	−81
Oct. 10, 1958	−85	−78	−88
Sept. 12, 1963	−45	−24	−68
Aug. 29, 1965	−58	−69	24
July 27, 1967	296	198	103
Sept. 16, 1969	−32	−2	30
Aug. 4, 1971	32	−4	−48
Aug. 18, 1972	−27	−61	−25
Sept. 5, 1973	−47	−3	−33
Oct. 22, 1974	92	26	114
Oct. 19, 1975	−34	11	104
Sept. 29, 1977	83	—	—
Chocolay			
Oct. 29, 1958	−43	−32	−32
Oct. 23, 1961	−90	−91	−89
Aug. 24, 1966	−75	−53	−45
Aug. 4, 1970	−82	1	−7
Sept. 12, 1973	−94	−91	−96
Silver			
June 11, 1958	−63	−40	139
Oct. 6, 1961	−95	−85	−88
Aug. 10, 1966	−66	2	14
Aug. 23, 1969	−72	−70	124
July 27, 1972	−81	−95	−92
Aug. 29, 1973	−77	−58	−60
Sept. 18, 1974	76	72	169
Sept. 7, 1975	−1	51	−21
Aug. 15, 1976	57	−19	—
Sept. 17, 1977	−48	—	—
Iron			
Sept. 15, 1958	−36	−23	506
July 27, 1962	−91	−85	−76
July 12, 1967	−87	−14	11
June 29, 1971	−82	−99	−100
Aug. 9, 1972	−94	−99	−97
Brule			
April 13, 1959	−50	16	−90
May 10, 1962	69	231	204
July 11, 1965	−96	−94	−57
July 15, 1969	−95	−48	22
July 17, 1972	−94	−86	−93
July 29, 1974	−50	91	352
July 9, 1977	−69	—	—
Amnicon			
Sept. 25, 1958	−87	−86	−37
July 17, 1962	−85	−74	−20
May 1, 1967	−26	688	766
Oct. 27, 1971	−97	−97	−94
July 13, 1972	13	105	1874
June 15, 1975	−97	−81	−11

of 24.4% of the index barrier catch of sea lampreys in 1967 and a low of less than 0.1% in 1974 (Table 3). The river was treated in 1971 and again in 1972 to destroy the ammocoete population and test the hypothesis that multiple treatments of streams with no offshore or lentic populations would destroy the ability of the stream to attract adult migrants. No larvae residual to the 1972 chemical treatment were found. After treatments in 1971 and 1972, the catch at the barrier declined from 1518 in 1971 to 16 migrant sea lampreys in 1973 (Table 1). The catch since 1972 fluctuated from 1 to 66 migrant sea lampreys, and in percentage contribution to the total index barrier catch from 0.1 to only 1.6 (Table 3). The numbers of sea lampreys attracted to the Iron River declined the year after each treatment (Table 1). In the 5 years before 1972, the barrier catch from this river averaged 12.6% of the total Lake Superior catch. The treatments of the Iron River in 1971 and 1972 unquestionably reduced the attraction of the stream to adult migrants.

After the 1972 treatment of the Iron River, the Salmon Trout River, about 5 km to the west, showed a noticeable increase in numbers of sea lamprey ammocoetes. For example, the number of larvae collected with electric shockers in the Salmon Trout River in the 5-yr period before 1971 ranged from 0 to 35 larvae/h (average, 12/h) and for the next 5 years ranged from 5 to 118/h (average, 69/h). Perhaps the adult sea lampreys which would have normally migrated into the Iron River were attracted to other streams in the area.

SILVER RIVER

The Silver River empties into Huron Bay, a long narrow bay that provides extensive lentic habitat for larval lampreys. Catches of sea lampreys at the electric barrier operating since 1954 varied from 5052 in 1961 to 117 in 1974 (Table 1). The catch in 1972 was 26.5% of the entire number captured at all barriers, whereas in 1959 the Silver River contributed only 2.4% (Table 3).

The Silver River was chemically treated 11 times to destroy the ammocoete populations. A decline in number of sea lampreys captured at the barrier occurred each year after the first six treatments of the stream (Table 1). A population of sea lamprey larvae exists off the mouth of the river in Huron Bay. To reduce recruitment to the Huron Bay population, the Silver River was treated each August or September from 1973 to 1978 to destroy the young-of-the-year larvae before they move downstream. In 1972 the barrier captured 2574 sea lampreys, 495 in 1973, and since has fluctuated from 117 to 312.

BRULE RIVER

The Brule River has five lakes in the headwaters and several lakelike impoundments (Bean and Thomson 1944). The upper reaches of the stream have a relatively flat profile but the gradient becomes steeper as the stream flows in a northerly direction towards Lake Superior. The mouth of the Brule River is from 30 to 34 km east of the mouths of two larger streams, the St. Louis and Nemadji rivers, and 16 km east of the medium-sized Amnicon River. Pollution probably deterred sea lampreys from the St. Louis River. The Nemadji River, for reasons unknown, attracts only small numbers of sea lampreys. The Iron River, about 16 km east of the Brule River, has no history of sea lamprey utilization and no known factor that would repulse spawning sea lampreys.

The largest catch of sea lampreys recorded at a barrier operating on Lake Superior was in the Brule River (22 593) in 1958 (Table 1). The Brule River was treated in April 1959, May 1962, and in July 1965, 1969, 1972, 1974, and 1977 (Table 4). Dates of treatments were sufficiently early in the year to allow resistant stages of the larvae to escape the treatments and for late spawning adults to repopulate the stream. Consequently, year-classes of ammocoetes became established after treatments.

The Brule River was treated below the uppermost range of sea lamprey ammocoetes in 1959 and 1962. In 1965 the entire area infested with larval sea lampreys was treated, and the catch declined from 6163 in 1965 to 226 in 1966. Since 1965, for 2–3 years after each treatment, the runs of adults into the Brule River increased until the stream was retreated, after which there was a reduction in numbers of sea lamprey captured at the barrier (Table 1). These data suggest that as ammocoete numbers increased between chemical treatments, the attraction for adults increased.

AMNICON RIVER

The watershed of the Amnicon River is between two larger river systems — the Brule River, about 16 km to the east, and the Nemadji River, about 16 km to the west. A natural barrier to the upstream migration of sea lampreys is located about 16 km above the mouth of the Amnicon River.

The catch of 11 038 sea lampreys at the electrical barrier on the Amnicon River in 1957 was exceeded only by catches from the barrier on the Brule River (Table 1). A significant decline in numbers captured usually occurred the year after a chemical treatment of the Amnicon River (Table 1). This stream was treated in 1971 and 1972. The catch of lampreys after the 1971 treatment declined from 4324 in 1971 to 132 in 1972, but increased to 149 in 1973. Only 80 sea lampreys were captured at the barrier in 1976.

PERCENTAGE CONTRIBUTION BY STREAMS TO SEA LAMPREY CATCH EACH YEAR

Percentage contribution of sea lampreys captured by streams to the total catch at the eight index barriers along the south shore of Lake Superior changed among years and streams (Table 3). The Brule River contributed 65.5% of the total number of sea lampreys captured in 1964, compared with only 3.5% in 1970. In 1975 the catch on the Amnicon River contributed 58.1% of the total, but the next year after treatment the contribution fell to 3.8%. Six of the index streams on Lake Superior usually declined in their ability to attract adult migrants the year after chemical treatment (Table 4) — the Amnicon River showed the highest decline (97%).

TREATMENT SUCCESS IN RELATION TO SIZE OF ADULT RUNS

The size of the adult run of sea lampreys the year after chemical treatment, in many instances reflects the success of the treatment. Streams where a complete kill of the ammocoete population is possible usually show a dramatic decline in numbers of adults using the stream a year later (Table 1). The number of adults captured increased after a partial treatment of the Brule River in 1962. The catch from the barrier in 1962 contributed 27.7% of the total catch at the eight index barriers, whereas in 1963 the contribution of the Brule River catch increased to 40.9% of the Lake Superior total. The adult run into the Brule River after the first complete treatment in 1965 declined from 6163 in 1965 to 226 in 1966. (Treatments of the Brule River in 1959 and 1962 were below the upstream distribution of the ammocoete population.) There appears to be a relation between the degree of success of a treatment and the number of adults that use the Brule River the year after each treatment.

Populations of larvae exist in lentic areas off the mouths of some streams and in inland lakes within a stream system. Where offshore or inland lake populations of larvae are present, annual treatments of the streams are undertaken to eliminate the larval populations in the streams before the ammocoetes move downstream into the lentic habitat. Streams with offshore or lentic populations do not show as great a decline in numbers of adult sea lampreys captured at

TABLE 5. Number and percentage change in the sea lamprey catch for streams with electric barriers which were treated in the same month on the south shore of Lake Superior from the total taken the year of chemical treatment to the total taken 1, 2, and 3 yr later, 1958–78. (Number of chemical treatments in parentheses of the 28 streams with electric barriers.)

	Sea lamprey catch						
Month of chemical treatments	Same year	1 yr		2 yr		3 yr	
		Number	% change	Number	% change	Number	% change
April (3)	19 746	10 076	−51	22 596	14	2 145	−89
May (7)	4 969	5 284	6	8 985	80	8 304	67
June (10)	14 314	9 716	−32	12 055	−16	12 344	−14
July (20)	26 827	6 172	−77	10 704	−60	18 436	−31
August (19)	9 018	8 104	−10	6 890	−23	7 255	−19
September (21)	25 981	9 758	−62	8 663	−67	17 891	−31
October (15)	36 951	10 322	−72	16 533	−55	14 835	−60

the barriers the year after a treatment as do streams that do not have associated offshore populations. The Silver and Sucker rivers contain associated lentic populations, and repetitive treatments failed to reduce the attraction to spawning migrants to the extent indicated in streams where no lentic populations were present. After the completion of the first round of treatments, no large runs of adult sea lampreys occurred in tributaries of the Upper Great Lakes unless some ammocoetes were present.

Usually, the later in the season a stream is treated (July through October) the greater effect the treatment has on the size of the adult run the following year (Table 5). Lampricide treatments in these months were most effective in destroying the larval populations of sea lampreys as the spawning run of adults was over, groundwater from spring runoff was eliminated, and young-of-the-year larvae were past their resistant stage.

The effects of a lampricide treatment on adult sea lampreys attracted to a stream after the chemical clears the river are unknown. Treatment of a stream during the spawning season kills the adult sea lampreys in the stream. At times, large numbers of adult sea lampreys were captured at barriers after a treatment during the period of migration. However, numbers of adults migrating into a stream occasionally declined after treatment. The cause of the decline has not been determined, but could result from factors other than those brought about by the treatment.

Discussion

The ability of the lamprey to select and use specific streams is well documented in the extensive ammocoete surveys of streams tributary to the Great Lakes (Torblaa and Westman 1980). A total of 424 streams tributary to Lake Superior contain the physical characteristics required by sea lampreys for spawning; however, ammocoetes have been found in only 119 streams (Smith et al. 1974). The number of streams containing ammocoetes of the sea lamprey has been reduced as control measures caused a reduction in adult populations. Several factors that may influence the use of a stream by sea lampreys are discussed.

HOMING

Homing behavior, or some equally important characteristic of the sea lamprey, would seem essential to the survival and perpetuation of the species. Skidmore (1959) attempted to answer the question: If sea lampreys on their spawning run of a river are captured and released in the lake, will they return to their stream of capture? On July 1, 1958, he released 159 spawning-run sea lampreys caught in the Pancake River at eight locations in Lake Superior to determine if they would return to the river. Of the 34 animals recaptured, less than half returned to the Pancake River, indicating that less homing can be anticipated later in the spawning run. Applegate and Smith (1951) reporting on the dispersion of spawning-run sea lampreys partly obstructed from entry into the upper Cheboygan River, a tributary of Lake Huron, found that the diverted lampreys moved in all directions from the tagging site.

Prior to the successful control of sea lampreys in the Upper Great Lakes, runs of adults were observed spawning in streams where little or no production of larvae occurred. The number of streams on Lake Superior where adults were observed outnumbered streams which contained ammocoete populations (Moore and Braem 1965). During the late 1950s and early 1960s in Lake Superior, the food supply for parasitic sea lampreys diminished (Pycha and King 1975), and the average size of the sea lamprey declined (Heinrich et al. 1980). Large numbers of lampreys, combined with a low food supply, undoubtedly caused stress to the population. With the successful control program and the recovery of the lake trout population, the spawning runs of lampreys are utilizing only the productive streams (Torblaa and Westman 1980). Apparently, the "healthier" adult sea lamprey is able to select the stream where reproduction has the best chance of being successful.

If homing does occur, application of lampricides could interfere with, or destroy factors which are used by the lamprey to select streams. Consequently, after a successful chemical treatment, adult sea lampreys that originated from the treated stream would not be able to locate the parent stream. Sea lampreys could be homing to streams after partial treatment if the stream still contains the attracting factors; however, because of the lack of evidence or data to support homing tendencies, we have not discussed this further.

TEMPERATURE

Applegate (1950), Wigley (1959), and Beamish and Potter (1975) considered temperature an important factor in selection of a spawning stream, for at least the landlocked sea lamprey. McLain et al. (1965) stated, "A few sea lampreys, although sporadic in their appearance at the barriers, can be expected as the mean daily water temperature in streams reach and exceed 4.5°C." Upstream movement increases considerably after 10°C is reached, generally during the 1st or 2nd wk of May (Smith 1962). The temperatures of most streams along the south shore of Lake Superior are within the range of 4–10°C when sea lampreys begin their selection of a stream for spawning. Although stream temperature is critical during the spawning act, it appears unlikely that temperature can be used as a major factor in selection of a specific stream for spawning (Hasler 1966). During the last weeks of the spawning run, temperatures are sufficiently diverse to enable sea lampreys to select the warmer streams. Selection of the warmer streams could prove disastrous if stream temperatures rise above the limits which can be tolerated by the ammocoete during the first 3 weeks of development. Whether temperature is a factor in the selection of a stream for spawning is unknown; however, other factors may prevent the sea lamprey from selecting streams that are excessively cold or warm.

STREAM FLOW

After the effects of sea lamprey control became evident by the sharp decline in numbers of sea lamprey in 1962, a large number of small streams ceased to attract adult sea lamprey. Factors other than stream size were also evident, as Purvis (1979) reported, "The decline in the catch of adult sea lampreys in 1962 was accompanied by a 30% decrease in the number of streams infested. Most of these streams have serious limiting factors such as cold water, steep gradient, limited spawning grounds, little larval habitat, or physical barriers to upstream migration."

Flow or size of a stream has not been a major determinant on the number of sea lamprey captured at an electric barrier (Table 3). The largest catches were made from the Brule River (22 593 in 1958), the Amnicon River (11 038 in 1957), followed by the Chocolay River (8088 in 1957). The Iron River, Bayfield County, Wisconsin, which flows into Lake Superior about 16 km east of the Brule River, has the same median flow as the Brule River. No sea lamprey was captured in the weir operated on the Iron River in 1958, and none have been observed in this stream. The fact that it does not attract sea lamprey indicates, at least in this area, that flow is not an important factor used by adult sea lamprey in locating a spawning stream.

The flow from a stream could contain attractants which may be used by adult sea lamprey to locate suitable streams for spawning. Consequently, we assume, or the consensus is, that the larger streams will attract greater numbers of adults if the factors are present. However, some of the larger streams on Lake Superior do not have spawning runs.

WATER QUALITY

Kleerekoper (1972) states, "The preponderance of the olfactory brain in lampreys as well as the very high specialization of the olfactory apparatus lead to the obvious conclusion that olfaction is the most important sensory system in these animals."

A lampricide treatment of a stream possibly reduces or eliminates a prime factor used by the sea lamprey to select a stream suitable for successful spawning and reproduction. Perhaps residual trace quantities of lampricides left in a stream after treatment could repel adult sea lamprey for a period. However, Teeter (1980) suggests that this is unlikely, as aged water treated with 5 μg TFM/g or less neither attracted nor repelled sexually mature lamprey. Most certainly any residual amounts of TFM, especially the year following a treatment, would be much less than 5 μg/g and should thus have no repellent effect on adults.

Pollution probably averts sea lamprey from a number of streams on the Great Lakes. However, sea lamprey were established in a tributary of the Oconto River, Lake Michigan, which was heavily polluted. Applegate (1950) stated, "In the Manistique River, Schoolcraft County, below the paper mill in that stream, sea lamprey enter channels in the estuary which carry a very heavy suspension of wood pulp waste. Furthermore, upon reaching the paper mill which blocks the river, large numbers of sea lamprey formerly entered a pipe discharging the combined hot pond and plant sewage wastes, and traversed this pipe to reach a small seepage channel (Weston Creek) above the mill." Sea lamprey spawn in Weston Creek and may use this route to bypass the dam. If conditions are satisfactory, sea lamprey will swim through heavily polluted areas to spawn. Although sea lamprey are tolerant of many pollutants and appear to be repelled by others, they are found in greatest abundance in streams of high water quality.

REDUCTION OF FLORA AND FAUNA

Lampricide treatments may in some way(s) change or reduce the flora or fauna within a stream which adults use as clues to stream selection. TFM could decrease the population of some species in the stream that takes a relatively long time to return to normal, and which adults can detect before entering a stream. Reductions in numbers and inhibition of growth, especially in diatoms and insects, were documented by Maki et al. (1975) and Torblaa (1968). However, in most if not all instances, the reductions were of short duration and the populations recovered within a year. Accelerated growth of ammocoetes after treatments would indicate the food supply of ammocoetes is not adversely affected (Purvis 1979). Therefore, it does not appear that a reduction in flora or fauna by lampricide treatments would affect the size of the migrating run of sea lamprey the year after a treatment.

EFFECTS OF AMMOCOETE POPULATIONS ON SPAWNING RUNS

A successful chemical treatment destroys most of the sea lamprey ammocoetes in a stream. Populations of ammocoetes of the native lampreys (*Ichthyomyzon* spp.) and American brook lamprey (*Lampetra lamottei*) are frequently found in the stream after application of lampricides (Schuldt and Goold 1980). Of the eight streams with index barriers, only the Amnicon River does not contain a population of native lampreys. A number of streams along the south shore of Lake Superior contain native lampreys (Moore and Braem 1965) and have no runs of sea lamprey. Larvae of the native species probably are not a major factor in attracting adult sea lamprey to a stream.

Teeter (1980) observed that "sexually immature male sea lampreys captured during a spawning migration showed significant preferences for water from tanks which contained sea lamprey ammocoetes." Furthermore, increasing the number of ammocoetes seemed to increase the preference. It is likely that the removal of a larval sea lamprey population from a stream by a lampricide treatment is a major factor that explains the decline in the adult run of sea lamprey in many streams the following year. If treatment is not entirely successful, the number of residual ammocoetes may influence the size of the adult run the next year. As the ammocoete population increases again in the years after a successful treatment, the attraction to adult sea lamprey also increases. Although migrant sea lamprey appear to be attracted by an established population of sea lamprey ammocoetes, a few adults enter streams that do not contain, or contain very few sea lamprey ammocoetes.

In a stream that is treated successfully, there is a dramatic decline in the numbers of migrant sea lamprey entering that stream the year after treatment. Although sea lamprey feeding in the lake are not affected by the chemical, the adult run into some streams was reduced by as much as 99% the year after a successful treatment, and was evident especially in streams which were treated later in the year. Also, the effect appears to be greater in streams which have no known lentic populations of larval sea lamprey.

APPLEGATE, V. C. 1950. Natural history of the sea lamprey, *Petromyzon marinus*, in Michigan. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 55: 237 p.

APPLEGATE, V. C., J. H. HOWELL, J. W. MOFFETT, B. G. H. JOHNSON, AND M. A. SMITH. 1961. Use of 3-trifluoromethyl-4-nitrophenol as a selective sea lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 1: 35 p.

APPLEGATE, V. C., AND B. R. SMITH. 1951. Movement and dispersion of a blocked spawning run of sea lampreys in the Great Lakes. Trans. North Am. Wildl. Nat. Resour. Conf. 16: 243–251.

BEAMISH, F. W. H., AND I. C. POTTER. 1975. The biology of the anadromous sea lamprey (*Petromyzon marinus*) in New Brunswick. J. Zool. London 177: 57–72.

BEAN, E. F., AND J. W. THOMSON JR. 1944. Topography and geology of the Brule River basin. Trans. Wis. Acad. Sci. Arts Lett. 36: 7–17.

GAYLORD, W. E., AND B. R. SMITH. 1966. Treatment of East Bay, Alger County, Michigan, with toxaphene for control of sea lampreys. U.S. Fish Wildl. Serv. Invest. Fish Control 7 (Resour. Publ. 11): 7 p.

HASLER, A. D. 1966. Underwater guideposts: homing of salmon. Univ. Wisconsin Press, Madison, Milwaukee, and London. 155 p.

HEINRICH, J. W., J. G. WEISE, AND B. R. SMITH. 1980. Changes in biological characteristics of the sea lamprey (*Petromyzon marinus*) as related to lamprey abundance, prey abundance, and sea lamprey control. Can. J. Fish. Aquat. Sci. 37: 1861–1871.

HOWELL, J. H., E. L. KING JR., A. L. SMITH, AND L. H. HANSON. 1964. Synergism of 5,2′-dichloro-4′-nitrosalicylanilide and 3-trifluormethyl-4-nitrophenol in a selective lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 8: 21 p.

KLEEREKOPER, H. 1972. The sense organs, p. 373–404. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2. Academic Press, London and New York.

MAKI, A. W., L. E. GEISSEL, AND H. E. JOHNSON. 1975. Toxicity of the lampricide 3-trifluoromethyl-4-nitrophenol (TFM) to 10 species of algae. U.S. Fish Wildl. Serv. Invest. Fish Control 56: 17 p.

MCLAIN, A. L., B. R. SMITH, AND H. H. MOORE. 1965. Experimental control of sea lampreys with electricity on the south shore of Lake Superior, 1953–60. Great Lakes Fish. Comm. Tech. Rep. 10: 48 p.

MOORE, H. H., AND R. A. BRAEM. 1965. Distribution of fishes in U.S. streams tributary to Lake Superior. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 516: 61 p.

PIAVIS, G. W., AND J. H. HOWELL. 1975. Effects of 3-trifluoromethyl-4-nitrophenol (TFM) on developmental stages of the sea lamprey. U.S. Fish Wildl. Serv. Invest. Fish Control 64: 8 p.

PURVIS, H. A. 1979. Variations in growth, age at transformation, and sex ratio of sea lampreys reestablished in chemically treated tributaries of the Upper Great Lakes. Great Lakes Fish. Comm. Tech. Rep. 35: 36 p.

PYCHA, R. L., AND G. R. KING. 1975. Changes in the lake trout population of southern Lake Superior in relation to the fishery, the sea lamprey, and stocking, 1950–70. Great Lakes Fish. Comm. Tech. Rep. 28: 34 p.

SCHULDT, R. J., AND R. GOOLD. 1980. Changes in the distribution of native lampreys in Lake Superior tributaries in response to sea lamprey (*Petromyzon marinus*) control, 1953–77. Can. J. Fish. Aquat. Sci. 37: 1872–1885.

SKIDMORE, J. F. 1959. Biology of spawning-run sea lampreys (*Petromyzon marinus*) in the Pancake River, Ontario. M.Sc. thesis, Univ. Western Ontario, London, Ontario. 88 p.

SMITH, B. R. 1962. Spring and summer temperatures of streams tributary to the south shore of Lake Superior, 1950–60. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 410: 57 p.

SMITH, B. R., AND J. J. TIBBLES. 1980. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936–78. Can. J. Fish. Aquat. Sci. 37: 1780–1801.

SMITH, B. R., J. J. TIBBLES, AND B. G. H. JOHNSON. 1974. Control of the sea lamprey (*Petromyzon marinus*) in Lake Superior, 1953–70. Great Lakes Fish. Comm. Tech. Rep. 26: 60 p.

TEETER, J. 1980. Pheromone communication in sea lampreys (*Petromyzon marinus*): implications for population management. Can. J. Fish. Aquat. Sci. 37: 2123–2132.

TORBLAA, R. L. 1968. Effects of lamprey larvicides on invertebrates in streams. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 572: 13 p.

TORBLAA, R. L., AND R. W. WESTMAN. 1980. Ecological impacts of lampricide treatments on sea lamprey (*Petromyzon marinus*) ammocoetes and metamorphosed individuals. Can. J. Fish. Aquat. Sci. 37: 1835–1850.

WAGNER, W. C., AND T. M. STAUFFER. 1962. The population of sea lamprey larvae in East Bay, Alger County, Michigan. Pap. Mich. Acad. Sci. Arts Lett. 47: 235–245.

WIGLEY, R. L. 1959. Life history of the sea lamprey of Cayuga Lake, New York. U.S. Fish Wildl. Serv. Fish. Bull. 59: 559–617.

Changes in Biological Characteristics of the Sea Lamprey (*Petromyzon marinus*) as Related to Lamprey Abundance, Prey Abundance, and Sea Lamprey Control[1]

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Biological characteristics of adult sea lampreys, *Petromyzon marinus*, in the Great Lakes changed in response to lamprey and prey abundance and the chemical control program. Sea lampreys collected as early as 1947, through 1978, from southern Lake Superior, northwestern Lake Michigan, the Ocqueoc River and Canadian shore of Lake Huron, and the Humber River of Lake Ontario were analyzed. Generally, abundance of sea lampreys peaked in each lake before the chemical control program began. The annual mean lengths and weights were relatively low when lampreys were abundant and increased as the numbers were reduced by the control efforts. As an indication of the change in sea lamprey weight per unit change in length, annual $\log_{10}$ weight on $\log_{10}$ length equations were solved at the arbitrary length of 410 mm. The values were plotted against years for each lake and interpreted with respect to chemical treatment periods. All slopes were negative before the control period and positive thereafter. Sea lamprey lengths and weights were low when fish stocks in the Great Lakes were near depletion. As salmonids again became abundant through stocking, lampreys grew larger. In Lake Superior, where detailed records on lake trout abundance have been available since 1959, a significant relation exists between the changes in the sea lamprey estimated weight values at 410 mm and in lake trout abundance ($P < 0.01$). Male sea lampreys were the dominant sex when populations of the parasite were high. A shift to a preponderance of females occurred as lamprey abundance declined.

Key words: Petromyzon marinus, Salvelinus namaycush, abundance, sex ratio, weight–length relationship, chemical control

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Les caractéristiques biologiques de la grande lamproie marine adulte, *Petromyzon marinus*, dans les Grands Lacs ont changé en réponse à l'abondance des lamproies et des proies, et au programme de contrôle chimique. Des grandes lamproies marines recueillies dès 1947, jusqu'en 1978 inclusivement, dans le sud du lac Supérieur, le nord-ouest du lac Michigan, la rivière Ocqueoc et la rive canadienne du lac Huron, ainsi que la rivère Humber du lac Ontario ont été analysées. En général, l'abondance des lamproies avait atteint un sommet dans chaque lac avant le début du programme de contrôle chimique. Les longueurs et poids annuels moyens sont relativement bas quand les lamproies sont abondantes et augmentent à mesure que le nombre diminue par suite du contrôle. Comme indice du changement de poids par changement unitaire de longueur chez les lamproies, nous avons résolu les équations $\log_{10}$ du poids annuel par rapport au $\log_{10}$ de la longueur, à la longueur arbitraire de 410 mm. Les valeurs ont été portées contre les années pour chaque lac et interprétées en relation avec les périodes de traitement chimique. Toutes les pentes sont négatives avant le contrôle et positives après. Les longueur et poids des grandes lamproies marines sont bas quand les stocks de poissons

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des Grands lacs sont presque épuisés. A mesure que les saumons deviennent plus abondants par suite d'ensemencements, les lamproies atteignent une taille plus grande. Dans le lac Supérieur, où existent des dossiers détaillés sur l'abondance du touladi depuis 1959, il y a une relation significative ($P < 0,01$) entre les changements des valeurs estimées du poids des grandes lamproies marines à 410 mm et de l'abondance des touladis. En périodes d'abondance du parasite, les grandes lamproies marines mâles sont le sexe dominant. Avec une diminution d'abondance, il y a glissement vers un prépondérance de femelles.

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A landlocked form of the sea lamprey (*Petromyzon marinus*) has been present in Lake Ontario for over a century. Changes in the animal's biological characteristics have taken place during this time to adapt to an environment different from its native marine habitat. Mature adult sea lampreys from the marine environment average 830 mm and 925 g (Beamish 1979). Sea lampreys from the Great Lakes are smaller; lampreys captured in Carp Creek, Lake Huron, in 1947 (one of the first years a significant number of lampreys were sampled from a Great Lakes tributary) averaged 442 mm and 184 g, but as conditions changed, the length, weight, and sex ratio varied.

Samples of spawning-phase sea lampreys were collected annually beginning as early as 1944 from Great Lakes tributaries. Initial collections were made with mechanical weirs and traps, and then, beginning in 1952, an extensive network of electrical barriers was installed in the upper three lakes (McLain et al. 1965). Adults collected from the barrier network provided most of the data for studies of adult sea lamprey biology. Since 1975, portable assessment traps (Great Lakes Fishery Commission 1978) and dip nets supplemented the barrier data. Sea lamprey abundance and biological information from these sources were described in part by many authors (Applegate 1950; Applegate and Smith 1950, 1951; Smith 1971; Smith et al. 1974). Smith (1971) described the changes in abundance, size, and sex ratios of sea lampreys from Lake Superior, Green Bay (Lake Michigan), and the Ocqueoc River (Lake Huron) from 1947 through 1969.

We describe here the changes in relative abundance and biological characteristics of sea lampreys from southern Lake Superior, northwestern Lake Michigan, the Ocqueoc River and Ontario shoreline of Lake Huron, and the Humber River of Lake Ontario. The weight–length relation of adult sea lampreys (P. M. Haack, Great Lakes Fish. Comm., Ann Arbor, MI, Appendix VII, December 1970, mimeograph) from each lake, based on the years before and during the use of the selective lampricide 3-trifluoromethyl-4-nitrophenol (TFM), is discussed; and in Lake Superior, the correlation with lake trout (*Salvelinus namaycush*) abundance is demonstrated.

Collection and Analysis

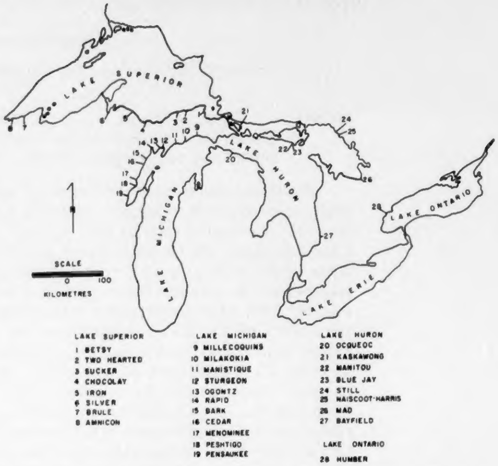

FIG. 1. Location of rivers tributary to the Great Lakes in which spawning-phase sea lampreys were collected for data on biological characteristics and abundance.

Electric barriers were initially operated in Lake Superior tributaries in 1953, and by 1958, 67 streams contained the devices. After the use of TFM for control of the sea lamprey in 1958 (Great Lakes Fishery Commission 1959), barrier numbers were gradually reduced. Assessment devices were operated on 24 streams from 1961 to 1967; this number was again reduced to 16 (all in the United States) in 1968–70, and by 1971 only 8 barriers remained in operation (Fig. 1, streams 1–8). Six of the eight barriers were operated annually from 1954 to 1978, and the Brule and Amnicon rivers provided data from 1957 to 1978. Data collected from Canadian barriers before 1967 indicated that the sea lampreys along the north shore were similar in size and sex composition to those in United States waters. Therefore, the longer series of data from the eight barriers along the south shore were used for discussions of Lake Superior sea lampreys.

Electric barriers, first installed in Lake Michigan tributaries in 1952, were operated in a maximum of 65 rivers in 1958, but by 1966, all were dismantled. Except for five streams in Green Bay and Hibbards Creek on the west shore, the devices were operated on most streams for only a few years. Information collected on biological characteristics and relative abundance of sea lampreys is fragmentary lakewide because of the short-term operation of most barriers; however, collections were more continuous from tributaries along the northwestern shore of Lake

Michigan. Data from 11 rivers along the northwestern shore (Fig. 1, streams 9–19) were used for discussion of sea lamprey characteristics. Although lampreys were not collected annually from each stream, sizable samples were obtained within the region from 1954 to 1966 with electric barriers, and in 1971 and 1974–78 by dip nets and portable assessment traps. Discussion of relative abundance is limited to the electric barrier catches from the Bark and Cedar rivers (Fig. 1, streams 15–16) for 1955–66.

A permanent sea lamprey barrier (mechanical 1948–51 and electrical 1952–78) was operated annually on the Ocqueoc River, Lake Huron (Fig. 1, stream 20), and provides relatively consistent data in all years except 1956 and 1958. Electric barriers were installed on two Ontario tributaries of Lake Huron in 1965, increased to seven by 1967 (Fig. 1, streams 21–27), and reduced to four in 1976. Collections for 1965–78 are used in this study.

Electric barriers were not operated on Lake Ontario tributaries; however, spawning-phase sea lampreys were collected annually from the Humber River (Fig. 1, stream 28) since 1968. Lampreys were captured at night below a dam about 4 km above the river mouth with long-handled dip nets.

Sea lampreys in this study were sampled from most streams over the entire spawning run. Sex was determined by examination of external secondary sexual characteristics when these were well developed, or by internal examination. Sea lampreys from Lakes Superior, Michigan, and the Ocqueoc River of Lake Huron were measured to the nearest millimetre; specimens from the Canadian collections of Lakes Huron and Ontario were recorded to the nearest 5 mm. Sexes were combined in all length and weight calculations.

Among the analyses of biological data were $\log_{10}$ weight on $\log_{10}$ length relationships. A convenient method to illustrate the changes that occurred in each lake was to solve each year's equation of log weight on log length for an arbitrary mean length of 410 mm. This length was selected because it is close to the yearly means of spawning run sea lampreys in the Great Lakes. Several lengths between 390 and 430 mm were examined and demonstrated the same trends. For each lake the logarithm of the annual estimate of weight for a 410-mm sea lamprey was plotted against year, and interpreted with respect to pre- and post-treatment periods. The criterion for determining pre- and post-control periods was based on the completion of the first series of treatments on all major sea lamprey producing tributaries within the sampling region of the lake plus 1 yr.

Size and Sex Composition of Great Lakes Sea Lampreys

Catches at electric barriers may not accurately reflect abundance of sea lampreys in the Great Lakes in all years but, in most cases, are the best long-term indicators available. Catches may be influenced by external factors such as: loss of electric power to the barrier, lampreys bypassing the device during floods, strong seiche action which transported immobilized individuals through an electrical field, low stream flow which may not attract migrating sea lampreys into the stream, and other temporary mechanical failures. In light of these factors, we use the term relative abundance in a very general sense and base its use on trends of total barrier counts over a minimum of 4 consecutive years (Table 1). Chemical control on Lake Superior tributaries began in 1958 and was intensified in the early 1970s by increasing the frequency of treatments on certain productive rivers. The long series of data from Lake Superior streams permitted a comparison of sea lamprey abundance with the intensity of chemical control.

LAKE SUPERIOR

Abundance of sea lampreys in Lake Superior was likely affected by the intensity of chemical control. An average of 39 136 sea lampreys were captured at the eight electric barriers from 1958 to 1961 and ranged from 27 057 in 1960 to 50 975 in 1961 (Table 1). The catch declined in 1962 (4 yr after the first lampricide treatments) to 7303 as a direct result of chemical treatments. Sea lamprey abundance apparently stabilized during the 4 years after the initial sharp decline and averaged 9115 for 1962–65, down 77% from the 1958–61 average. The number of spawning adults averaged 6604 in 1966–72, an 83% reduction from precontrol abundance. The average number from 1973 to 1978 was 3477, a further decline to 91% less than precontrol numbers.

The largest and smallest average weights of sea lampreys from Lake Superior were 218 g in 1954 and 133 g in 1961 (Table 2). The lowest average weight coincided with greatest lamprey abundance. Average weight steadily declined from 1954 to 1961, then increased until 1972. Weight thereafter varied little from 1973 to 1978, ranging from 161 g (1973 and 1978) to 179 g (1975).

Least squares fit of linear regression estimates of log weight, given mean length of 410 mm on years, was used to show trends in weight changes of Lake Superior sea lampreys (Fig. 2). In general, for sexes of lamprey combined, the log weight for a mean length of 410 mm decreased until 1962, the year after control had its greatest impact on population numbers. Values increased thereafter indicating the sea lampreys were becoming heavier in relation to length. Analysis of the values during pre- and post-control periods (1954–61 and 1961–78, respectively) shows correlations significant at $P < 0.01$ for both segments (Fig. 2) — 1954–61 and 1961–78. The slope was negative during the precontrol period, decreasing at a detransformed rate of 4.6 g/yr, and positive thereafter, increasing 0.9 g/yr.

A relation exists between abundance of sea lampreys and percentage of males in Lake Superior for 1958–78 (Tables 1 and 2) and is significant at $P < 0.01$ ($r = 0.624$). Males and females were about equally represented in the collections in 1955 (53% males), but males became increasingly dominant as lampreys increased. Abundance peaked in 1961, and the predominance of males was greatest in 1960–62 (68–71%). In 1962, barrier catches of sea lampreys in Lake Superior declined 86% from the previous year; the percentage of males began to decline in 1963. As abun-

TABLE 1. Annual catches of spawning-phase sea lampreys from selected Great Lakes tributary rivers, 1949–78.

Year	Lake Superior (8 electric barriers)	Lake Michigan (Bark and Cedar rivers)	Lake Huron (Ocqueoc River)	Lake Huron (Ontario barriers)	Lake Ontario (Humber River)
1949	—	—	24 643	—	—
1950	—	—	18 822	—	—
1951	—	—	19 393	—	—
1952	—	—	9 437	—	—
1953	—	—	11 676	—	—
1954	—	—	10 183	—	—
1955	—	15 744	13 683	—	—
1956	—	18 043	—	—	—
1957	—	14 672	8 163	—	—
1958	45 824	9 389	—	—	—
1959	32 688	7 903	2 766	—	—
1960	27 057	5 741	7 560	—	—
1961	50 975	10 508	4 715	—	—
1962	7 303[a]	6 439	5 205	—	—
1963	8 366	6 710	4 674	—	—
1964	10 249	3 770	2 677	—	—
1965	10 540	2 765[a]	1 390	937[b]	—
1966	4 091	774	3 273	3 555[c]	—
1967	2 630	—	674	6 272	—
1968	6 909	—	3 418	10 737	1191
1969	8 513	—	3 291[a]	4 782[a]	1366
1970	4 781	—	736[d]	1 588	2185
1971	9 613	—	2 997	2 043	2450
1972	9 696	—	2 847	1 503	4615
1973	2 847	—	639[d]	197	6308[a]
1974	1 911	—	910	225	3350
1975	4 395	—	1 900	333	6848
1976	2 098	—	6 947	461[e]	4030
1977	4 796	—	503[d]	1 020[e]	1601
1978	4 812	—	2 121	222[e]	2453

[a] The year the control program began showing an effect on the adult sea lamprey population.
[b] Catch from Still and Naiscoot–Harris rivers.
[c] Catch from Still, Naiscoot–Harris, Mad, and Bayfield rivers.
[d] Some escapement occurred because of equipment failure.
[e] Catch from Still, Naiscoot–Harris, Kaskawang, and Blue Jay rivers.

dance declined through the 1960s, so did the percentage of males, and by 1969, they accounted for only 28% of the spawning migrants captured. The sex ratio stabilized near 30% males during 1971–78. The ratio of males to females has stabilized at a lower level in Lake Superior than in any of the other lakes.

Covariance analysis was used to compare weight–length relationships between years, sexes, and streams (P. M. Haack, mimeograph). All logarithmic equations used in the analyses were statistically significant. Yet, it is very difficult to see any pattern involving individual streams, years, and sexes. For example, for 12 out of 13 yr there was a significant difference between slopes and adjusted means involving individual sexes in the Brule and Amnicon rivers. These rivers are only 24 km apart and usually have large runs of lampreys. The slopes and adjusted means were significantly different for each of the eight electric barrier streams compared over the years 1962–70; this held for individual sexes and sexes combined.

Lake trout abundance in Michigan and Wisconsin waters of Lake Superior was monitored closely from 1950 to 1978 (Pycha and King 1975; R. L. Pycha, U.S. Fish and Wildlife Service, Ashland, Wisconsin, personal communication). Briefly, severe sea lamprey predation beginning in the late 1940s, combined with intensive commercial fishing in the early 1950s, seriously depleted the lake trout stocks in Michigan and Wisconsin waters, and by 1960, abundance was at an all-time low (Pycha and King 1975). A combination of sea lamprey control, intensive stocking of lake trout, and restrictions on commercial fishing reversed this trend around 1962. Lake trout abundance increased through 1977 in Michigan waters, and 1970 in Wisconsin waters. Since 1971 this trend has again reversed in Wisconsin waters and in Whitefish Bay, at the extreme eastern end of the lake, due primarily to exploitation by a native American fishery on the United States side and a commercial fishery in Canadian waters (Smith and Tibbles 1980).

TABLE 2. Mean length and weight and percentage of males of sea lampreys collected from tributary rivers of the Great Lakes.

	Lake Superior (8 electric barriers)			Lake Michigan (Northwest Region)			Lake Huron (Ocqueoc River)			Lake Huron (Ontario barriers)			Lake Ontario (Humber River)		
Year	Length (mm)	Weight (g)	% males	Length (mm)	Weight (g)	% males	Length (mm)	Weight (g)	% males	Length (mm)	Weight (g)	% males	Length (mm)	Weight (g)	% males
1947[a]	—	—	—	—	—	—	442	184	63	—	—	—	—	—	—
1948[a]	—	—	—	—	—	—	426	—	63	—	—	—	—	—	—
1949	—	—	—	—	—	—	433	—	66	—	—	—	—	—	—
1950	—	—	—	—	—	—	418	—	70	—	—	—	—	—	—
1951	—	—	—	—	—	—	406	122	71	—	—	—	—	—	—
1052	—	—	—	—	—	—	402	130	70	—	—	—	—	—	—
1953	—	—	—	—	—	—	420	141	70	—	—	—	—	—	—
1954[b]	456	218	60	449	166	63	411	129	69	—	—	—	—	—	—
1955[b]	436	188	53	434	154	60	414	131	67	—	—	—	—	—	—
1956[b]	450	196	57	441	159	59	—	—	—	—	—	—	—	—	—
1957	431	168	58	430	152	65	411	126	60	—	—	—	—	—	—
1958	424	161	58	418	138	61	—	—	—	—	—	—	—	—	—
1959	428	162	58	449	173	60	402	124	58	—	—	—	—	—	—
1960	413	143	69	450	173	63	383	108	60	—	—	—	—	—	—
1961	408	133	68	415	125	65	408	126	57	—	—	—	—	—	—
1962	429	155	71	430	143	64	420	138	54	—	—	—	—	—	—
1963	425	156	68	417	126	68	—	—	—	—	—	—	—	—	—
1964	420	150	57	445	160	66	395	118	54	—	—	—	—	—	—
1965	430	159	54	439	161	59	433	157	51	413	162	46	—	—	—
1966	408	141	44	419	139	44	—	—	—	415	151	43	—	—	—
1967	420	161	38	—	—	—	—	—	—	420	154	47	—	—	—
1968	419	155	36	—	—	—	—	—	—	429	167	39	408	150	50
1969	417	157	28	—	—	—	409	133	46	428	158	43	414	160	51
1970	429	169	36	—	—	—	430	151	53	449	182	45	414	152	53
1971	448	190	37	469	211	43	445	180	44	465	199	46	410	149	56
1972	443	192	31	—	—	—	479	206	—	487	228	44	405	144	55
1973	421	161	31	—	—	—	428	160	38	474	211	42	409	150	55
1974	430	163	30	483	228	34	452	182	44	470	212	38	420	161	58
1975	434	179	31	480	248	33	458	200	31	483	230	39	432	183	54
1976	428	174	29	475	252	21	469	218	35	494	246	34	459	231	57
1977	431	173	30	477	253	45	486	236	37	482	226	37	467	235	54
1978	427	161	31	501	258	48	440	181	40	479	222	37	443	209	42

[a] Data for 1947–48 for Lake Huron from Carp Creek, a small tributary adjacent to the Ocqueoc River.
[b] Data for 1954–56 for Lake Superior from Betsy, Two Hearted, Sucker, Chocolay, Iron, and Silver rivers.

Comparison of the sea lamprey weight–length relations (log weight at 410 mm) each year correlated closely with the numbers of lake trout captured per 30 480 metres of gill net in the preceding year (Fig. 3 and 4). Correlation of lake trout abundance in Wisconsin waters with sea lamprey weight/mean length of 410 mm from the Amnicon and Brule rivers is significant at $P < 0.01$ ($r = 0.635$). A similar correlation of lake trout abundance in Michigan waters and sea lamprey weight/mean length of 410 mm from the Silver, Iron, Chocolay, Sucker, Two Hearted, and Betsy rivers shows significance at $P < 0.01$ ($r = 0.698$).

Lake trout have now been stocked in Lake Superior for over 30 yr — the first hatchery-reared fish were released in 1947 (Buettner 1961). A recent Michigan Department of Natural Resources creel census, showing lake trout contribute 53% of the sport fishing catch (A. T. Wright, Michigan DNR, Lansing, personal communication), may indicate lake trout dominance in the Lake Superior salmonid community. The changes in weight/mean length of 410-mm sea lampreys could be used as an indirect indicator of lake trout abundance in Lake Superior.

LAKE MICHIGAN

Sea lamprey control expanded to Lake Michigan in 1960, and a first round of treatments was completed on all streams by 1965 (Smith and Tibbles 1980). Most streams in the northwest region, including Green Bay, were treated once by 1963. The catch of sea lampreys at the electric weirs on the Bark and Cedar rivers declined 56% from 6710 in 1963 to 3770 in 1964 (Table 1). Only 774 adults were captured in 1966, the last year these weirs were operated.

The average weight of sea lampreys from northwest Lake Michigan from 1954 to 1963 (Table 2) — the years before chemical control measures — varied within

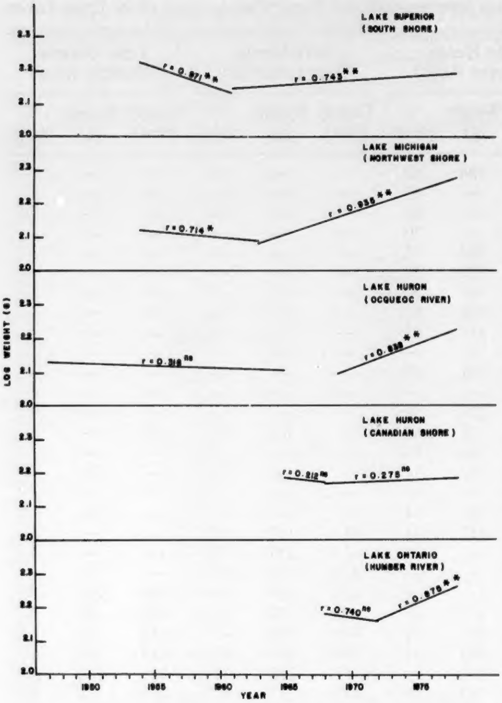

FIG. 2. Trends in regression values of weight at length of 410 mm of spawning-phase sea lampreys collected from the Great Lakes, 1947–78. The correlation coefficient *r* is an indicator of precision of these lines (ns $P > 0.05$, * $P < 0.05$, ** $P < 0.01$). Data not available for all years from each lake.

a fairly narrow limit and ranged from 125 g (1961) to 173 g (1959 and 1960). Average weight increased from 139 g (1966) to 258 g (1978) as lamprey abundance declined. The mean weight recorded in 1978 is currently the largest from any of the Great Lakes populations.

Changes in the percentage of males in the Lake Michigan lamprey population, in response to chemical control, were similar to those in Lake Superior. The percentage of males generally increased from 1954 (low in 1956, 59%) to a high of 68% in 1963 (Table 2), thereafter male abundance declined to a low of 21% of the population in 1976. This trend reversed in 1977 and 1978, rising to 45% and 48%, respectively. The overall trend in sex ratio is inversely proportional to the changes in average weight. The lack of relative abundance data after 1966 made any comparison between abundance and changes in the sex composition impossible.

The changes in log weight at a mean length of 410 mm from Lake Michigan sea lampreys were similar to the variations in average weight. Analysis of the estimates from pre- and post-control periods showed significant correlations (Fig. 2); the first segment (1954–63) significant at $P < 0.05$ and the second segment (1963–78) significant at $P < 0.01$. Estimated weight at 410 mm decreased at a detransformed rate of 1 g/yr from 1954 to 1963, then increased 4.1 g/yr from 1963 to 1978.

Lake trout were virtually eliminated from Lake Michigan by 1950 (Lawrie 1970). Restocking to rehabilitate the population began in 1965, and commercial fishing for lake trout was prohibited in Lake Michigan waters. Lakewide growth and survival of planted trout were high and lake trout once again became abundant (Wells and McLain 1973), but the absence of firm estimates of abundance precludes any comparison with changes in sea lamprey size. The relative abundance of all salmonids, including the recently introduced Pacific salmon (coho, *Oncorhynchus kisutch*, and chinook, *O. tshawytscha*) can be inferred from a Wisconsin Department of Natural Resources creel census conducted from 1969 to 1977. The total sport salmonid catch along the Wisconsin shore rose from about 15 t in 1969 to 189 t in 1974, declined to 92 t by 1976, then rose to an all-time high of 282 t in 1977. Lake trout contributed from 9% (1969) to 37% (1971) of this catch, with the largest numbers taken in 1974 (38 t, or 20% of the total catch). Pacific salmon, coho and chinook, contributed 30% (1970) to 54% (1977) of the sport catch in Wisconsin waters during this same period.

The initial decrease and then increase in the log weight at a 410-mm mean length of sea lampreys in Lake Michigan appear to follow closely the decline of the lake trout and subsequent rebuilding of a salmonid base. The smallest annual weight estimate at 410 mm occurred in 1961, before lake trout and other salmonids were reintroduced into Lake Michigan. As the stocks of salmonids became increasingly more abundant in recent years, especially larger fish, the log weight at the selected length of sea lamprey steadily increased (Fig. 2).

LAKE HURON

Ocqueoc River — Catches from the Ocqueoc River represent the longest continuous record of a precontrol sea lamprey population. State of Michigan biologists installed a weir and trap on the river in 1944 and 1945 to study the biology of sea lampreys (Shetter 1949). This structure proved inefficient and a permanent weir and trap were installed in 1949 and operated each year except 1956 and 1958 (Smith 1971). The catch of 24 643 adult sea lampreys taken in 1949 is the largest recorded in the Ocqueoc River and apparently represented the peak of sea lamprey abundance in Lake Huron. Catches generally declined from 1949 to 1955 (Table 1) and averaged 15 411, with a low of 9437

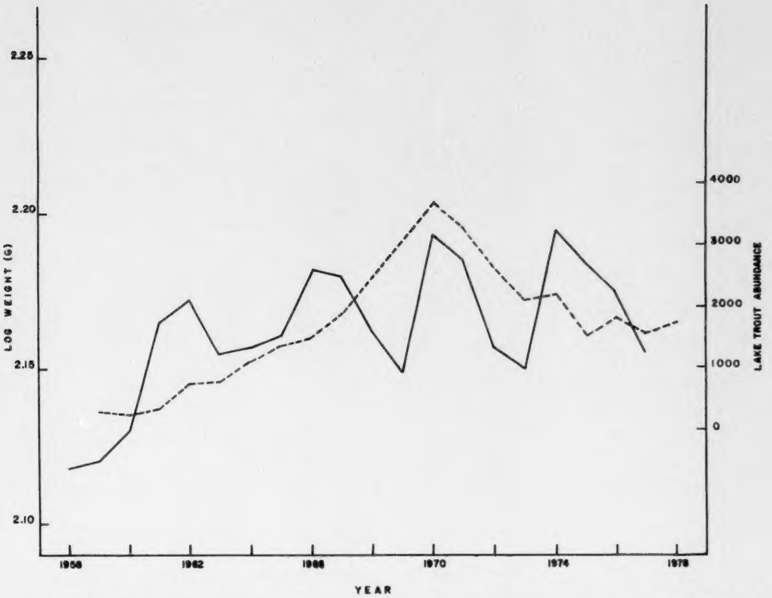

FIG. 3. Relation between the number of lake trout >432 mm caught per 30 480 m of assessment gill net from Wisconsin waters of Lake Superior (broken line), and the estimated log weight at 410 mm for sea lampreys captured in the Brule and Amnicon rivers (solid line), 1959–78. Data as graphed adjust to the fact that spawning lampreys captured in the spring of year $t + 1$ were feeding mostly on lake trout in year t.

in 1952. The numbers varied widely thereafter, but continued in a general downward trend for the next several years. Catches averaged 4984 from 1959 to 1963, and 2454 from 1964 to 1969.

All sea lamprey streams tributary to the North Channel and Georgian Bay, as well as three tributaries to the U.S. side of the St. Marys River, were treated between 1960 and 1962 (Great Lakes Fishery Commission 1961, 1962). Chemical treatments in Lake Huron were interrupted in 1961 in Canada and in 1962 in the United States, but were continued in 1966, and by 1968, the majority of Lake Huron streams were treated once. The catch at the Ocqueoc River after chemical treatments (1969–78) fluctuated without trend (range, 503–6947).

A significant correlation exists between the percentage of males and sea lamprey numbers in the Ocqueoc River runs. As abundance declined from 1949 to the late 1960s, the percentage of males declined (Tables 1 and 2). From 1950 to 1953 males represented more than 70% of the population, but began to decline thereafter and continued gradually downward to 50% in 1965. The shifting of the sex composition as early as the mid-1950s, even before the beginning of chemical treatments in Lake Huron tributaries, suggests a response to undefined environmental conditions. Applegate (1950) indicated that some unknown factors may have been influencing the sex and size of sea lampreys from the Ocqueoc River even before 1949. Both sex ratio and abundance seemed to vary without trend after 1969. Males increased to 53% of the population in 1970, declined to 38% by 1973, rose to 44% in 1974, fell to 31% in 1975, then steadily increased to 40% by 1978. The relation between abundance and numbers of males was significant at $P < 0.01$ ($r = 0.736$).

Average weight of sea lampreys from the Ocqueoc River remained relatively constant from 1951 until 1969 (the year chemical treatments should have begun to affect the population) and ranged from 108 to 157 g. During the control years, average weight steadily increased from 133 g in 1969 to 236 g in 1977, but declined again to 181 g in 1978.

The slope of the regression of log weight at 410 mm (Fig. 2) was not significant from 1947 to 1965, but was significant from 1969 to 1978 ($P < 0.01$). Estimated weight at 410 mm decreased at a detransformed rate of 0.4 g/yr for the first segment and increased 3.4 g/yr during the second.

Although data on abundance of lake trout and other salmonids in Lake Huron were not available until recently, some inferences can be made from fish stocks

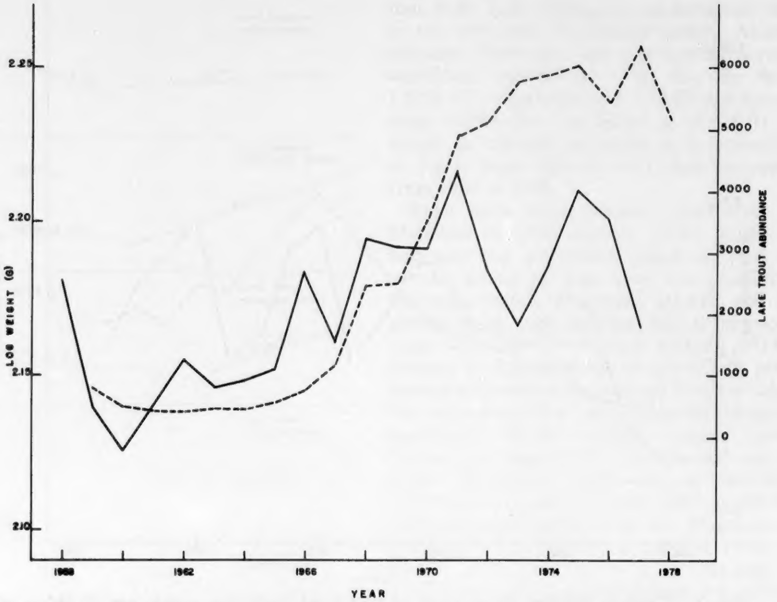

FIG. 4. Relation between the number of lake trout >432 mm caught per 30 480 m of assessment gill net from United States waters of Lake Superior east of the Keweenaw Peninsula (broken line), and the estimated log weight at 410 mm for sea lampreys captured in the Betsy, Two Hearted, Sucker, Chocolay, Iron, and Silver rivers (solid line), 1959–78. Data as graphed adjust to the fact that spawning lampreys captured in the spring of year $t + 1$ were feeding mostly on lake trout in year t.

and sea lamprey data from the Ocqueoc River. Lake trout were virtually eliminated from Lake Huron by the early 1950s (Lawrie 1970). The average weight of adult sea lampreys from Carp Creek, a small Lake Huron tributary adjacent to the Ocqueoc River, in 1947 was 184 g. During the same year, the commercial production of lake trout from Lake Huron amounted to 177 t. The commercial catch in 1959 was less than 0.5 t; sea lamprey average weight decreased to 108 g in the Ocqueoc River in 1960. Lake trout were absent through the 1960s as the size of adult sea lampreys remained small. Coho and chinook salmon were planted in Lake Huron between 1963 and 1969 and lake trout stocking began in U.S. waters in 1973 (Great Lakes Fishery Commission 1969, 1970, 1975). Sea lampreys began to increase in size in 1971, coinciding with reports of heavy scarring on chinook salmon along the west shore of Lake Huron.

Ontario Shore — Electric barriers were first operated along the eastern shore of Lake Huron in 1965 (Table 1). Spawning runs of sea lampreys were sampled from two tributaries of Georgian Bay, the Still and Naiscoot–Harris rivers (Fig. 1, streams 24–25). Another tributary of Georgian Bay, the Mad River (Fig. 1, stream 26), and the Bayfield River (Fig. 1, stream 27) of the lake proper were added in 1966. Barriers were operated on seven tributaries in 1967, with the addition of weirs on three other streams (Fig. 1, streams 21–23). The Mad, Manitou, and Bayfield River barriers were discontinued in 1976.

The numbers of sea lampreys taken at these Canadian barriers steadily increased from 1966 to a peak of 10 737 in 1968, and averaged 6337 from 1966 to 1969. Following the first round of lampricide treatments in Lake Huron, the numbers of lampreys captured at the weirs declined sharply and averaged 1331 in 1970–73 and 452 in 1974–78 (a final reduction of 93% of the 1966–69 average). The elimination of the three barriers in 1976 did not significantly influence the resulting data because their contribution to the total catch for 1971–75 was less than 4% of the total barrier catch.

Average weight of lampreys collected between 1965 and 1970 ranged from 151 to 167 g (Table 2). As lampreys became less abundant through the control program, their average weight increased to 228 g by 1972. Weights decreased slightly to 211 and 212 g in

TABLE 3. Number (in thousands) of splake and lake trout planted in Ontario waters of Lake Huron, 1969–78.[a]

Year	Splake	Lake trout
1969	35	0
1970	247	0
1971	468	0
1972	333	0
1973	412	0
1974	299	0
1975	523	0
1976	658	0
1977	940	15
1978	174	15

[a] Data from K. H. Loftus, Ontario Ministry of Natural Resources, Toronto, Ont., personal communication.

1973 and 1974, respectively, but rose again to 230 g in 1975. Average weight ranged from 222 to 246 g from 1975 to 1978.

Although average weight increased after the start of chemical control, the annual weight–length relation expressed as log weight at 410 mm varied only slightly from a computed low of 143 g in 1971 to a high of 162 g in 1976. The relations were not significant during either pre- or post-control periods (Fig. 2). Estimated weight at 410 mm decreased at a detransformed rate of 1.5 g/yr before TFM treatments and increased 0.5 g/yr after control.

The percentage of males captured in the eastern Lake Huron electric barriers showed a general downward trend, from 47% in 1967 to 34% in 1976, but increased to 37% in 1977 and 1978 (Table 2). This trend is similar to the Ocqueoc River data for the same period. No significant correlation exists between the sex ratio of sea lampreys and their abundance as measured by the electric barrier catches.

The Province of Ontario began stocking splake (*Salvelinus namaycush* × *S. fontinalis*) in Lake Huron as early as 1966. Plantings after 1968 were of a stock selected (F_5-generation splake) for fast maturation and a habitat preference to the areas and depths formerly used by lake trout. These splake were stocked in Ontario waters from 1969 to 1978, and in addition, 30 000 lake trout were planted in South Bay, Manitoulin Island, in 1977–78 (Table 3). The weight–length relation of sea lampreys varied only slightly during 1969–78, and the number of splake planted from 1970 to 1974 remained relatively constant, but fluctuated considerably from 1975 to 1978.

LAKE ONTARIO

Humber River — The numbers of sea lampreys captured at the Humber River from 1968 to 1978 varied without any apparent correlation to lamprey size, prey numbers, or control (Table 1). A first round of lampricide treatments was completed early in the summer of 1972. Catches steadily increased from 1191 in 1968 to 6308 in 1973 and averaged 3019. In 1974 the numbers declined to 3350, but increased in 1975 to 6848, declined in 1977 to 1601, again increased in 1978 to 2453, and averaged 3656 for the period. These data from this one river may not be indicative of lakewide sea lamprey abundance. Lamprey scarring on salmon in Lake Ontario has decreased dramatically, suggesting a marked decline of the parasite within recent years (Pearce et al. 1980).

Average weight of sea lampreys varied slightly from 1968 to 1973 (Table 2), ranging from 144 g in 1972 to 160 g in 1969. Average weight thereafter steadily increased to a high of 235 g by 1977.

A reduction of the estimated weight at 410 mm of sea lampreys collected from the Humber River occurred before the start of control, followed by a sharp increase from 1973 to 1978. Analysis of the values of weight at 410 mm based on pre- and post-control periods (Fig. 2) showed no significant trend for the first segment, 1968–72, but a significant trend from 1972 to 1978 ($P < 0.01$). Estimated weight at 410 mm decreased at a detransformed rate of 1.8 g/yr before lampricide treatments and increased thereafter at 5.6 g/yr.

The percentage of male sea lampreys in the Humber River ranged from 50 to 58 in 1968–77 (Potter et al. 1974; Great Lakes Fishery Commission 1978). Females predominated for the first time in 1978 as male abundance dropped to 42%. No correlation exists between the percentage of males in the spawning population and the average weight or abundance.

Following the initial small plants of chinook and coho salmon by the Province of Ontario in 1968 and New York State in 1970, stocking increased steadily, and in 1978 more than 2.4 million trout and salmon were planted in Canadian and United States waters of Lake Ontario (Great Lakes Fishery Commission, March, 1979, mimeograph). The resultant large salmonid base in the lake, coupled with the chemical control program, undoubtedly contributed to the recent increases in sea lamprey growth.

FACTORS AFFECTING SIZE OF SEA LAMPREYS IN THE GREAT LAKES

Sea lampreys in the Great Lakes were always smaller than those migrating into rivers of the Atlantic Coast of North America. Lampreys collected from Love Lake Outlet of the East Machias River in Maine in 1960–64 averaged 663 mm and 737 g (Davis 1967). The largest spawning migrants recorded from the Great Lakes averaged 501 mm and 258 g from Lake Michigan in 1978.

At least three interrelated factors have influenced sea lamprey size: (1) lamprey abundance, (2) the effectiveness of the chemical control program, and (3) the availability of preferred host species. Sea lampreys entered the Upper Great Lakes when food was abundant and grew to a substantial size. Growth of lampreys decreased and lake trout stocks were depleted as the abundance of lampreys increased. As the use of the selective lampricide began, large-scale stocking of trout and salmon also began to rehabilitate the salmonid stocks quickly. The control program significantly reduced lamprey numbers and the salmonid stocking increased prey species. Lamprey size began to increase as a result and, after a period of years, generally stabilized.

TRENDS OF SEX COMPOSITION IN SEA LAMPREY OF THE GREAT LAKES

Most authors reported that in typical spawning populations of lampreys, particularly of nonparasitic species, an excess of males is present (Hardisty and Potter 1971; Potter et al. 1974; Potter and Beamish 1977). All sea lamprey populations in the Great Lakes exhibited a dominance of males in spawning populations before they were subjected to an effective sea lamprey control program.

Whether sea lampreys were endemic to Lake Ontario (Christie 1972) or became established after the opening of the Erie Canal (Smith 1972) has been discussed for many years, but is not particularly relevant to a discussion of the changes caused by sea lamprey control. In either case, sea lampreys have been present in Lake Ontario since the 1830s (Lark 1973) and probably represented a stable landlocked population. Sampling of the spawning run in the Humber River indicated the sex composition in Lake Ontario was male dominant and remained reasonably constant during the precontrol period. Beamish (1980) reported a similar sex composition in native anadromous sea lampreys in the St. Johns River, New Brunswick.

Sea lampreys were relatively recent intruders into Lakes Superior, Michigan, and Huron, and the ratio of males to females in the population apparently varied in response to the changes in lamprey abundance. Comparisons of the corresponding data from both Lakes Superior and Huron showed that males were the dominant sex when lampreys were abundant. In all three upper lakes, as the sea lamprey populations declined with the advent of the lampricide program, the sex composition began to shift from a preponderance of males to an excess of females. As each population reached a level of 30–40% males, the ratio stabilized. The application of the lampricides reduced the population of sea lampreys in the lakes and contributed to the sequential shifting of the sex composition from a predominance of males to an excess of females.

Acknowledgments

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APPLEGATE, V. C. 1950. Natural history of the sea lamprey, *Petromyzon marinus*, in Michigan. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 55: 237 p.

APPLEGATE, V. C., AND B. R. SMITH. 1950. Sea lamprey spawning runs in the Great Lakes, 1950. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 61: 49 p.

1951. Sea lamprey spawning runs in the Great Lakes, 1951. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 68: 37 p.

BEAMISH, F. W. H. 1979. Migration and spawning energetics of the anadromous sea lamprey, *Petromyzon marinus*. Environ. Biol. Fish. 4: 3–7.

1980. Biology of the North American anadromous sea lamprey, *Petromyzon marinus*. Can. J. Fish. Aquat. Sci. 37: 1924–1943.

BUETTNER, H. J. 1961. Recoveries of tagged, hatchery-reared lake trout from Lake Superior. Trans. Am. Fish. Soc. 90: 404–412.

CHRISTIE, W. J. 1972. Lake Ontario: effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 913–929.

DAVIS, R. M. 1967. Parasitism by newly-transformed anadromous sea lampreys on landlocked salmon and other fishes in a coastal Maine lake. Trans. Am. Fish. Soc. 96: 11–16.

GREAT LAKES FISHERY COMMISSION. 1959, 1961, 1962, 1969, 1970, 1975, 1978. Annual Reports. Great Lakes Fish. Comm., Ann Arbor, MI.

HARDISTY, M. W., AND I. C. POTTER. 1971. The behaviour, ecology and growth of larval lampreys, p. 85–125. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London and New York.

LARK, J. G. I. 1973. An early record of the sea lamprey (*Petromyzon marinus*) from Lake Ontario. J. Fish. Res. Board Can. 30: 131–133.

LAWRIE, A. H. 1970. The sea lamprey in the Great Lakes. Trans. Am. Fish. Soc. 4: 766–775.

MCLAIN, A. L., B. R. SMITH, AND H. H. MOORE. 1965. Experimental control of sea lampreys with electricity on the south shore of Lake Superior, 1953–60. Great Lakes Fish. Comm. Tech. Rep. 10: 48 p.

PEARCE, W. A., R. A. BRAEM, S. M. DUSTIN, AND J. J. TIBBLES. 1980. Sea lamprey (*Petromyzon marinus*) in the lower Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1802–1810.

POTTER, I. C., AND F. W. H. BEAMISH. 1977. The freshwater biology of adult anadromous sea lampreys, *Petromyzon marinus*. J. Zool. London 181: 113–130.

POTTER, I. C., F. W. H. BEAMISH, AND B. G. H. JOHNSON. 1974. Sex ratios of adult sea lampreys, *Petromyzon marinus*, from a Lake Ontario tributary. J. Fish. Res. Board Can. 31: 122–124.

PYCHA, R. L., AND G. R. KING. 1975. Changes in the lake trout population of southern Lake Superior in relation to the fishery, the sea lamprey, and stocking, 1950–70. Great Lakes Fish. Comm. Tech. Rep. 28: 34 p.

SHETTER, D. C. 1949. A brief history of the sea lamprey problem in Michigan waters. Trans. Am. Fish. Soc. 76: 160–176.

SMITH, B. R. 1971. Sea lampreys in the Great Lakes of North America, p. 207–247. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London and New York.

SMITH, B. R., AND J. J. TIBBLES. 1980. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936–78. Can. J. Fish. Aquat. Sci. 37: 1780–1801.

SMITH, B. R., J. J. TIBBLES, AND B. G. H. JOHNSON. 1974. Control of the sea lamprey, *Petromyzon marinus*, in Lake Superior, 1953–70. Great Lakes Fish. Comm. Tech. Rep. 26: 60 p.

SMITH, S. H. 1972. Factors of ecological succession in oligotrophic fish communities of the Laurentian Great Lakes. J. Fish. Res. Board Can. 29: 717–730.

WELLS, L., AND A. L. MCLAIN. 1973. Lake Michigan: Man's effects on native fish stocks and other biota. Great Lakes Fish. Comm. Tech. Rep. 20: 55 p.

Changes in the Distribution of Native Lampreys in Lake Superior Tributaries in Response to Sea Lamprey (*Petromyzon marinus*) Control, 1953–77[1]

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Populations of three species of lampreys, American brook lamprey (*Lampetra lamottei*), northern brook lamprey (*Ichthyomyzon fossor*), and silver lamprey (*I. unicuspis*), endemic to the Lake Superior drainage basin have declined since chemical control of the sea lamprey (*Petromyzon marinus*) was begun; 64% (103 of 162) of the streams inhabited by endemic species have required treatment. The parasitic silver lamprey was most adversely affected by lampricide applications. Though 4278 were captured at 35 of 55 Lake Superior barriers in 1959, a total of 91 were reported in only nine tributaries and the St. Marys River from 1973 to 1977. American brook lampreys were least affected by chemical control and have disappeared from 6 of 42 treated streams which they inhabited. *Ichthyomyzon* larvae are no longer found in 41 of 81 treated streams they once inhabited, though few larvae were found in many of these streams. Several factors affected the vulnerability of native lampreys to chemicals. Nonparasitic lampreys, especially American brook lampreys, inhabited headwater areas which were often not invaded by sea lampreys, but silver lampreys spawned in lower reaches and their entire stream distribution was exposed to the effects of the lampricide. Differences in fecundity of lampreys also affected their recovery after chemical treatments.

Key words: Ichthyomyzon fossor, Ichthyomyzon unicuspis, Lampetra lamottei, streams, distribution, habitat, temperature, fecundity, survival, TFM

SCHULDT, R. J., AND R. GOOLD. 1980. Changes in the distribution of native lampreys in Lake Superior tributaries in response to sea lamprey (*Petromyzon marinus*) control, 1953–77. Can. J. Fish. Aquat. Sci. 37: 1872–1885.

Depuis le début du contrôle chimique de la grande lamproie marine (*Petromyzon marinus*), les populations de trois espèces de lamproies, la lamproie de ruisseau américaine (*Lampetra lamottei*), la lamproie de ruisseau septentionale (*Ichthyomyzon fossor*) et la lamproie argenté (*I. unicuspis*), endémiques du bassin hydrographique du lac Supérieur, ont décliné; 64% (103 sur 162) des cours d'eau habités par des espèces endémiques ont dû être traités. La lamproie argentée parasite est celle qui a le plus souffert des applications de lampricide. Bien que 4278 sujets aient été capturés à 35 des 55 barrières du lac Supérieur en 1959, un total de 91 ont été signalés dans seulement neuf tributaires et dans la rivière St. Marys entre 1973 et 1977. La lamproie de ruisseau américaine a été la moins affectée par le contrôle chimique : elle a disparu de 6 des 42 cours d'eau traités qu'elle habitait. Les larves d'*Ichthyomyzon* ont disparu de 41 sur 81 cours d'eau traites qu'elles fréquentaient jadis, bien que quelques larves aient été trouvés dans plusieurs de ces cours d'eau. Plusieurs facteurs ont affecté la vulnérabilité des lamproies indigènes aux substances chimiques. Les lamproies non parasites, surtout la lamproie de ruisseau américaine, habitaient les régions de la tête des eaux qui, souvent, n'étaient pas envahies par la grande lamproie marine; par ailleurs, la lamproie argentée frayait dans la partie inférieure et leur entière distribution dans le cours d'eau était exposée aux effets du lampricide. Des différences dans la fécondité des espèces affectèrent aussi le rétablissement des lamproies après traitements chimiques.

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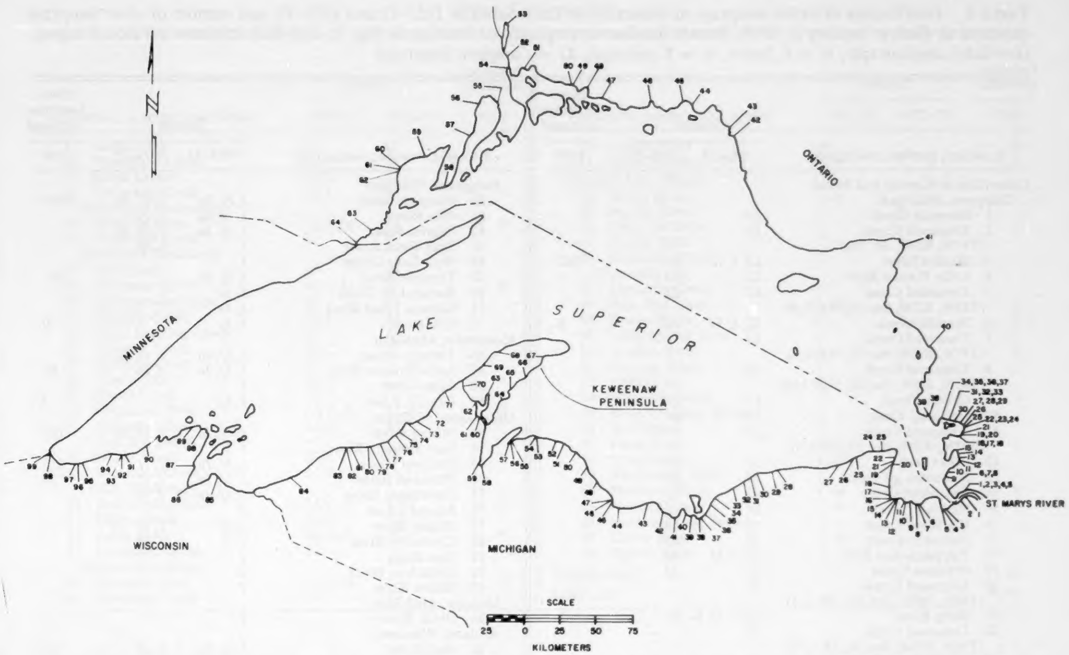

FIG. 1. Lake Superior, showing locations of 99 United States and 64 Canadian tributaries from which native lampreys were collected. (See Table 1 for names of streams and species collected.)

NATIVE lampreys were distributed throughout the Lake Superior drainage basin before the invasion of the sea lamprey (*Petromyzon marinus*). The only native parasite, the silver lamprey (*Ichthyomyzon unicuspis*), spawned occasionally in streams throughout the watershed but was most abundant along the southwestern shoreline. Northern brook lamprey (*I. fossor*) were most abundant in western streams and American brook lamprey (*Lampetra lamottei*) dominated eastern streams. The distribution of these species extended over much of east-central North America, but the use of lampricides since 1958 (Smith et al. 1974) has inadvertently destroyed many native lampreys and greatly decreased their distribution throughout the Great Lakes watershed.

In this paper changes in distribution of lampreys native to the Lake Superior drainage basin as determined from collections made incidentally to sea lamprey control from 1953 to 1977 (Table 1, Fig. 1) are described. The reasons for the varying degrees of vulnerability among these species to the chemical control of sea lampreys are also discussed. The reduction in the distribution of native lampreys in Lake Superior, due to chemical control, can serve as a model for the effects of lampricide treatments upon these species in other Great Lakes.

Materials and Methods

Initial attempts to control sea lampreys concentrated on installing barriers downstream of lower spawning grounds in streams to prevent sexually mature sea lampreys from reproducing. Mechanical weirs and traps were replaced with electric barriers in 1953. Eventually 97 streams were included in the network, 60 in the United States and 37 in Canada. The barrier program provided much information on the abundance and distribution of silver lampreys, the only native lampreys large enough to be retained effectively in barrier traps (McLain et al. 1965). Collections from electric barriers on 55 Lake Superior tributaries in 1959 provided estimates of pretreatment populations of silver lampreys.

Lamprey larvae were collected during the stream surveys carried out with electroshockers or lampricides to determine the presence of sea lamprey ammocoetes in tributaries of Lake Superior. Electric generators were used from 1955 to 1958, then were replaced by portable, battery-powered, alternating-current, backpack shockers (Braem and Ebel 1961; Tibbles 1961) which, in turn, were replaced by transistorized, direct-current, backpack units in 1968. Each modification of equipment increased the efficiency of the collecting procedure. Since 1966, a formulation of the molluscicide, 2-aminoethanol salt of 2′,5-dichloro-4′-nitrosalicylanilide as a 5% active ingredient on silica sand (Bayer 73), has been used for surveying larval habitat in deep and turbid water. All streams were surveyed peri-

TABLE 1. Distribution of native lampreys in tributaries to Lake Superior 1953–72 and 1973–77, and number of silver lampreys captured at electric barriers in 1959. Stream number corresponds to location in Fig. 1, and dash indicates no recent survey. (*I* = *Ichthyomyzon* spp., *If* = *I. fossor*, *Iu* = *I. unicuspis*, *Ll* = *Lampetra lamottei*.)

Location, number, and stream	Species		Silver lampreys captured
	1953–72	1973–77	1959
United States (County and State)			
Chippewa, Michigan			
1 Seymour Creek	*Ll*		
2 Unnamed Creek	*Ll*		
(T47N, R1W, Sec 16)			
3 Waiska River	*Ll, I, Iu*	*Ll*	161
4 Little Waiska River	*Ll*	*Ll*	
5 Unnamed Creek	*Ll*	*Ll*	
(T47N, R2W, Sec 30, NE 1/4)			
6 Pendills Creek	*Ll, I, Iu*	*Ll*	5
7 Unnamed Creek	*Ll*	—	
(T47N, R4W, Sec 29, NE 1/4)			
8 Unnamed Creek	*Ll*	—	
(T47N, R4W, Sec 29, NW 1/4)			
9 Grants Creek	*Ll*	*Ll*	
10 Halfaday Creek	*Ll*	*Ll*	
11 Unnamed Creek	*Ll*	—	
(T47N, R5W, Sec 15, SE 1/4)			
12 Mill Creek	*Ll*	*Ll*	
13 Naomikong Creek	*Ll*	*Ll*	
14 Ankodosh Creek	*Ll*	*Ll*	
15 Roxbury Creek	*Ll*	*Ll*	
16 Big Silver Creek	*Ll*	*Ll*	
17 Galloway Creek	*Ll*	*Ll*	
18 Tahquamenon River	*Ll, I, If*	*Ll*	
19 O'Briens Creek	*Ll*	*Ll*	
20 Unnamed Creek	*Ll*	—	
(T49N, R6W, Sec 10, NE 1/4)			
21 Betsy River	*Ll, I, If, Iu*	*Ll*	2
22 Unnamed Creek	*Ll*	—	
(T50N, R6W, Sec 14, SE 1/4)			
23 Weatherhog Creek	*Ll*	—	
24 Vermilion Creek	*Ll*	—	
Luce, Michigan			
25 Three Mile Creek	*Ll*	*Ll*	
26 Little Two Hearted River	*Ll*	*Ll*	0
27 Two Hearted River	*Ll, Iu*	*Ll*	1
Alger, Michigan			
28 Sucker River	*Ll, Iu*	*Ll*	1
29 Sable Creek	*Ll*	*Ll*	
30 Hurricane Creek	*Ll*	*Ll*	0
31 Sullivans Creek	*Ll*	*Ll*	
32 Seven Mile Creek	*Ll*		
33 Beaver Lake Outlet	*Ll*	*Ll*	
34 Mosquito River	*Ll*		
35 Miners River	*Ll*	*Ll*	0
36 Munising Falls Creek	*Ll*	*Ll*	
37 Tannery Falls Creek	*Ll*	—	
38 Anna River	*Ll*	*Ll*	
39 Furnace Creek	*Ll, Iu*	*Ll*	1
40 Five Mile Creek	*Ll*	*Ll*	
41 Au Train River	*Ll, I, If, Iu*	*Ll, I, If*	1
42 Rock River	*Ll*	*Ll*	0
43 Laughing Whitefish River	*Ll, I, If*	*I, If*	0
Marquette, Michigan			
44 Chocolay River	*Ll, I, If, Iu*	*Ll*	0
45 Carp River	*Ll, I*	*Ll*	0
46 Whetstone Creek	*Ll*	—	
47 Dead River	*I, If*	*I, If*	
48 Harlow Creek	*Ll, I, If, Iu*	*I*	0
49 Big Garlic River	*Ll, Iu*		2
50 Iron River	*Ll, I, If, Iu*	*I, If*	13
51 Salmon Trout River	*I, If, Iu*		10
52 Pine River	*I, If, Iu*	*I*	24
53 Little Huron River	*I*	*I*	
54 Huron River	*I, If, Iu*		27
Baraga, Michigan			
55 Ravine River	*I, If, Iu*	*I, I,*	16
56 Slate River	*I, If*	*I, If*	
57 Silver River	*I, If, Iu*	*I, If, Iu*	49
58 Falls River	*I, Iu*		
59 Six Mile Creek	*I*		
Houghton, Michigan			
60 Sturgeon River	*I, If, Iu*	*I, If, Iu*	1913
61 Pike River	*I, If, Iu*	*I, If*	
62 Pilgrim River	*I, If, Iu*	*I, If, Iu*	
63 Trap Rock River	*I*	*I, If*	
64 Mud Lake Outlet	*I*		
65 Traverse River	*I, If, Iu*		65
70 Boston-Lily Creek	*I, Iu*	*I*	
71 Salmon Trout River	*I, Iu*		
72 Elm River	*I, Iu*		0
Keweenaw, Michigan			
66 Tobacco River	*I, If, Iu*	*I, If, Iu*	
67 Little Gratiot River	*I, If, Iu*	*I, Iu*	64
68 Eliza Creek	*I*		
69 Gratiot River	*I, Iu*		3
Ontonagon, Michigan			
73 Misery River	*I, If, Iu*	*I, If, Iu*	186
74 East Sleeping River	*I*		
75 Firesteel River	*I, If, Iu*	*I, If*	215
76 Flintsteel River	*I, If, Iu*	*I, If*	15
77 Ontonagon River	*I, If, Iu*	*I, If*	
78 Second Creek	*I*		
79 Potato River	*I, If*	*I, If*	
80 Cranberry River	*I, If*	*I, If*	
81 Iron River	*I*		
82 Little Iron River	*I*		
83 Union River	*I*		
Gogebic, Michigan			
84 Black River	*I*		
Ashland, Wisconsin			
85 Bad River	*I, If, Iu*	*I, If*	90
Bayfield, Wisconsin			
86 Fish Creek	*I, If, Iu*	*I, If, Iu*	103
87 Sioux River	*I*		
88 Raspberry River	*I*		
89 Sand River	*I*	*I, If*	
90 Cranberry River	*I, Iu*		5
91 Iron River	*I, Iu*		
92 Reefer Creek	*I, Iu*		
93 Fish Creek	*I, Iu*		
Douglas, Wisconsin			
94 Brule River	*I, If, Iu*	*I, Iu*	633
95 Poplar River	*I, If, Iu*		106
96 Middle River	*I, If, Iu*	*I, If*	376
97 Amnicon River	*I, If, Iu*	*Iu*	146
98 Nemadji River	*I, If, Iu*	*I*	5
99 St. Louis River			
United States total			4238
Canada (District and Province)			
Algoma, Ontario			
1 East Davignon Creek	*Ll*	*Ll*	
2 West Davignon Creek	*Ll*	*Ll*	
3 Unnamed Creek	*Ll*	—	
(Korah Township)			
4 Little Carp River	*Ll, I, Iu*	*Ll*	0
5 Big Carp River	*Ll, I, Iu*	*Ll*	0
6 Unnamed Creek	*Ll*	—	
(Prince Township)			
7 Unnamed Creek	*Ll*	—	
(Prince Township)			
8 Unnamed Creek	*Ll*	—	
(Dennis Township)			
9 Kellys Creek	*Ll*	—	
10 Unnamed Creek	*Ll, I*	—	
(Pennefather Township)			
11 Cranberry Creek	*Ll, I, Iu*	*Ll*	
12 Goulais River	*Ll, I, Iu*	*Ll*	
13 Unnamed Creek	*Ll*	—	
(Fenwick Township)			
14 Bostons Creek	*Ll*	*Ll*	

TABLE 1 (*Concluded*)

	Species		Silver lampreys captured
Location, number, and stream	1953–72	1973–77	1959
15 Kars Creek	*Ll*	*Ll*	
16 Horseshoe Creek	*Ll, I*	*Ll*	
17 Black Creek	*Ll, I*	*Ll*	
18 Unnamed Creek (Havilland Township)	*Ll, I*	*Ll*	
19 Stokeley River	*Ll, I, Iu*	*Ll*	0
20 Unnamed Creek (Havilland Township)	*Ll*	*Ll*	
21 Tier Creek	*Ll*	*Ll*	
22 Harmony River	*Ll, I, Iu*	*Ll*	0
23 Government Creek	*Ll*	*Ll*	
24 Sawmill Creek	*Ll, I*	*Ll*	
25 Jones Landing Creek	*Ll*	*Ll*	
26 Downey Creek	*Ll, I*		
27 Garbage Creek	*Ll*		
28 Tiny Creek	*Ll, I*		
29 Nixon Creek	*Ll, I*	—	
30 Chippewa River	*Ll, I, Iu*	*Ll, I*	16
31 Unnamed Creek (Tilley Township)	*Ll, I*	*Ll*	
32 Unger Creek	*Ll, I*	*Ll*	
33 Unnamed Creek (Tilley Township)	*Ll, I*	—	
34 Batchawana River	*Ll, I, Iu*	*Ll, I*	6
35 Digby Creek	*Ll, I*	*Ll*	
36 Sable River	*Ll, I, Iu*	*Ll, I*	0
37 Unnamed Creek (Fisher Township)	*Ll*		
38 Pancake River	*Ll, I, Iu*	*Ll*	1
39 Westman Creek	*Ll*	*Ll*	
40 Agawa River	*Iu*		0
41 Michipicoten River	*I, Iu*	*I*	3
Thunder Bay, Ontario			
42 White River	*I, Iu*		
43 Big Pic River	*I*	*I*	
44 Little Pic River	*I*		
45 Prairie River	*I, Iu*	*I*	
46 Unnamed Creek (Township 82)	*I*	—	
47 Hewitson Creek	*I*	—	
48 Pays Plat River	*I, Iu*	*I*	0
49 Gravel River	*I*	*I*	0
50 Little Gravel River	*I*		0
51 Jackfish River	*I*	*I*	0
52 Nipigon River	*I*	*I*	
53 Cash Creek	*I*		
54 Stillwater Creek	*I*		
55 Black Sturgeon River	*I*	*I*	
56 Wolf River	*I*		
57 Pearl River	*I*	*I*	
58 Sibley River	*I, Iu*	*I*	
59 MacKenzie River	*I*	*I*	
60 McIntyre River	*I, Iu*	*I*	9
61 Neebing River	*I, Iu*	*I*	5
62 Kaministikwia River	*I*	*I*	
63 Cloud River	*I, Iu*		
64 Pigeon River	*I*		
Canada total			40
Lake total			4278

odically, but most emphasis was placed upon streams which currently contain or have contained sea lamprey larvae. Information on endemic lampreys has been gathered incidentally to the collection of sea lampreys.

Stream treatments with lampricides, 3-trifluoromethyl-4-nitrophenol (TFM) and a mixture of TFM and powdered Bayer 73, provided an additional source of lampreys. Samples were collected with modified fyke nets and dip nets at stations throughout treated portions of the stream. The percentage of the population that was sampled decreased as the size of the treated stream increased (Smith and McLain 1962), and was generally quite small. Although more than 710 000 native larvae were collected from Lake Superior streams since 1953, precise comparison of ammocoete numbers from year to year is lacking because of the many variables associated with different gears and annual changes in amount of effort. Collection data, however, do show changes in relative abundance of native lampreys.

Larval lampreys of the genera *Lampetra* and *Ichthyomyzon* were also destroyed during early treatments (Applegate et al. 1961) and were thought to exhibit no substantial difference from sea lampreys in susceptibility to the lampricide. Sea and native lampreys were used in bioassays to determine treatment concentrations of TFM (Howell and Marquette 1962). Recent evidence indicates that sea lampreys are most susceptible to TFM, American brook lampreys the least susceptible, and *Ichthyomyzon* of intermediate susceptibility (Davis 1970). Though sea and American brook lampreys exhibit the widest range in susceptibility, the difference is not enough to permit selective removal of sea lampreys (Dawson et al. 1975).

The upstream distribution of sea lamprey larvae in tributaries where chemicals have been applied was a critical factor in reducing native populations. Originally decisions to treat streams were based upon the collection of even a single sea lamprey larva. The need for additional guidelines to determine treatment schedules soon became apparent and now several factors are considered, the more important being the size, growth rate, and abundance of sea lamprey ammocoetes in each stream. TFM applications are more frequent in streams with problem areas such as lakes, long estuaries, beaver ponds, and springs which provide for escapement of larvae (Smith et al. 1974).

Lampricide application sites are located upstream from sea lamprey infestation. The chemical was sometimes applied upstream of known sea lamprey infestation at more readily accessible locations, if the upstream limits of sea lampreys were in doubt.

The length of stream in which larvae were found was determined by following the course of the stream with a map measurer and included the distance from the mouth to the farthest upstream collection site. Stream flows were the average flows at which streams were treated (Smith et al. 1974). Stream numbers in the text refer to the locations in Fig. 1. The use of native ammocoetes in mark and recapture studies and bioassays has led to some establishment outside of the normal range. These larvae generally were destroyed in subsequent treatments and were not used to determine distribution in this report.

Native lampreys were considered eliminated from a stream if none were collected from 1973 to 1977. Surveys between treatment years in Canada were not as intensive as those in the United States. Since all Canadian stream survey data were not available, status of these streams was determined mainly from collections made during treatments.

American Brook Lampreys

DISTRIBUTION AND HABITAT

American brook lampreys are presently confined to the eastern half of Lake Superior. Their distribution was previously described in Canada as extending westward to Westman Creek (No. 39; W. B. Scott, Great Lakes Research Committee, 1954, Appendix 9, mimeograph). Scott and Crossman (1973) reported one larva from Wolf River (No. 56) in 1949, but none were collected since sea lamprey control was initiated. The previous western limit in the United States was extended 14 km from the Big Garlic River (No. 49; Moore and Braem 1965) to the Iron River (No. 50). Fifteen larvae were captured in 1970 during surveys of the Iron River and one was recovered during the 1971 treatment. The origin of these larvae remains a mystery as the nearest source of American brook ammocoetes in 1970 was the Chocolay River (No. 44), 51 km east of Iron River.

American brook lampreys inhabited 88 streams (39 in Canada and 49 in the United States) tributary to Lake Superior (Table 1). Moore and Braem (1965) documented this species in 38 United States streams, and since then many small streams ($\leq$1.6 km long) which contained few American brook larvae have been added. American brook lampreys were most common in small, cold, clear Lake Superior tributaries, but were recovered from streams with flows ranging from 0.03 to 17 m^3/s. This species was also common in the St. Marys River which contains the entire outflow of Lake Superior (2123 m^3/s; United States Department of Commerce 1974). Maximum summer temperatures in the St. Marys River rarely exceeded 18.3°C. Along the south shore of Lake Superior, maximum summer temperatures (10-d averages) were generally five Celsius degrees lower in eastern streams than in western streams (Smith 1962). American brook lampreys were common in Halfaday Creek (No. 10) where maximum summer temperatures reached just 10.6°C (10-d average).

CHANGES IN POPULATIONS

American brook larvae were established throughout about 600 km in streams along the United States shoreline before chemical control of the sea lamprey. Chemical treatments were conducted over 500 km (83%) of this distance since 1958. Though American brook larvae declined with each treatment, this species showed much more resiliency than *Ichthyomyzon* spp. and repopulated streams which were only occasionally treated.

TFM was applied to 42 (13 in Canada and 29 in the United States) of the 88 streams inhabited by American brook lampreys. This native species disappeared from six of these streams, all in the United States (Table 2).

TABLE 2. Number of American brook larvae and their distribution prior to the disappearance of ammocoetes from six United States streams. (Stream number corresponds to location on Fig. 1.)

Stream number and name		Distribution (km)	Number collected	Years of collections
32	Seven Mile Creek	7.0	160	1958–68
34	Mosquito River	2.7	746	1958–69
43	Laughing Whitefish River	5.9	1	1961
48	Harlow Creek	2.4	18	1962–65
49	Big Garlic River	3.9	277	1959–63
50	Iron River	4.3	16	1970–71
Total		26.2		

American brook lampreys were common in three of the streams from which they have disappeared. Few larvae were collected from the Laughing Whitefish (No. 43, 1) and Iron (No. 50, 16) rivers and Harlow Creek (No. 48, 18); however, during initial treatment years on the Mosquito (No. 34) and Big Garlic (No. 49) rivers and Seven Mile Creek (No. 32), this species comprised 98, 58, and 48%, respectively, of all lamprey larvae collected. Three treatments eliminated this species from the Mosquito and Big Garlic rivers and Seven Mile Creek.

Although the decline of American brook lampreys over much of its range in the Lake Superior drainage basin seems solely attributable to TFM, pollution may have played a role in the decline of this species in the Carp River (No. 45). Sterba (1962) felt that even slight pollution may destroy a population of lamprey larvae. During the only treatment (1963) of the Carp River, 440 American brook larvae were netted, 97% of all lamprey larvae collected. Since this treatment, 81 larvae have been collected, the last in 1973. It is uncharacteristic that one treatment can eliminate this species, and pollution by sewage treatment facilities may have resulted in the demise of this population.

Effects of lampricide — A case history — Though American brook larvae were eliminated from few streams and have repopulated streams occasionally treated, the total number of larvae has been drastically reduced and the distribution greatly decreased in streams frequently treated. The effects of frequent chemical treatments upon this species are demonstrated by comparing collections during the first and last treatment years (Table 3) in the Two Hearted River (No. 27). The number of collection stations was comparable in 1959 and 1975.

The Two Hearted River contained one of the largest populations of American brook lampreys along the southern Lake Superior shoreline. Larvae were scattered throughout the 67.2 km of main stream and were present in many of the tributaries. Six treatments were conducted to control sea lampreys (1959, 1962, 1965, 1970, 1973, and 1975). Similar portions of the stream were treated in 1959 and 1975. An additional 1.6 km of the North Branch and 3.2 km of the South Branch were treated in 1959 but not treated in 1975; however,

TABLE 3. Numbers and percentage of American brook lampreys and sea lampreys collected in the Two Hearted River in 1959 and 1975.

	1959			1975		
	American brook lampreys collected			American brook lampreys collected		
Location of collection	Number	Percentage	Number of sea lampreys collected	Number	Percentage	Number of sea lampreys collected
Mouth to East Branch	919	92	76	8	9	84
East Branch to junction of Dawson Creek	358	54	309	0	0	32
Dawson Creek to junction of North Branch	1	100	0	1	<1	124
East Branch	2759	99	10	733	91	69
Wabash and Johns Creek	0	0	2	0	0	0
Dawson Creek	270	65	145	1	1	90
North Branch	55	59	39	0	0	18
West Branch	85	97	3	44	92	4
South Branch	44	96	2	12	63	7
Total	4491	88	586	799	65	428

9.6 km more of the East Branch were treated in 1975.

The reduction of native lampreys is most noticeable from the lower sections of large streams since these areas are treated more frequently and are farther from sources of recruitment. The section from the mouth to the junction of East Branch accounted for 20% (919) of all American brook lampreys in 1959, but only 1% (8) in 1975. In the area from the junction of the East Branch to the junction of Dawson Creek, collections decreased from 358 (8%) to no larvae from 1959 to 1975. The percentage of American brook lampreys in the entire lamprey population declined from 92 to 9 and from 54 to 0, respectively, in these two zones.

The survival of native lampreys in any section of a river depends upon whether sea lampreys can successfully reproduce there in numbers requiring lampricide applications. Stauffer and Hansen (1958) stated that sea lampreys were precluded from the East Branch by low water temperatures. About half of this tributary was treated before 1975, but sea lamprey larvae were discovered above this application point which necessitated treatment of an additional 10 km of stream. Most of the American brook larvae collected from the entire river were from the East Branch in 1959 (61%) and 1975 (92%). All but 3 of the 733 native larvae collected in the East Branch during 1975 were from the section receiving initial treatment. The number of American brook lampreys collected during chemical treatments declined 96% after 1959 in the rest of the Two Hearted River.

The reduction in the number of native lampreys and a shift to sea lampreys throughout this river are representative of other major river systems frequently treated. Few of the original areas inhabited by American brook lampreys in the Two Hearted River have gone untreated and they presently survive in scattered pockets in the treated portions and several small untreated tributaries. Although other large United States streams (No. 3, 26, 28, 41, and 44) contained plentiful American brook lamprey habitat, this species currently survives only in areas above the application points of the chemical, and in smaller untreated tributaries.

CURRENT STATUS

United States — American brook larvae are numerous in some treated and untreated streams along the United States shoreline. This species is abundant in 8 (No. 4, 5, 10, 12, 15, 16, 19, and 30) of 20 streams which were never treated. Five treated streams (No. 9, 13, 25, 36, and 38) apparently contain marginal sea lamprey habitat. When adult sea lampreys were numerous, they spawned in each of these streams which were subsequently treated once or twice. There has been no recent record of sea lamprey larvae in these small, cold streams where American brook larvae abound.

Adjacent lacustrine environments provide stocks of native lampreys which can quickly repopulate a stream following TFM applications; however, such areas also allow sea lampreys to escape treatment. Sea lamprey larvae apparently have a greater tendency to drift downstream than American brook ammocoetes. In 1955–56, larvae of this native species outnumbered sea lamprey ammocoetes 3 to 1 in the Sucker River (No. 28), yet were less numerous off the mouth (Wagner and Stauffer 1962).

Infrequent treatments of some streams with lentic environments (No. 13, 17, 36, and 38) caused temporary declines of native lampreys, but these streams were quickly repopulated by recruitment to adult stocks from offshore. Annual treatments of other streams (No. 28, 33, 39, and 41) to prevent downstream drift of sea lamprey ammocoetes have greatly decreased numbers of American brook larvae in offshore areas and lower sections of rivers.

American brook lampreys are afforded protection from TFM treatments upstream of four man-made and one natural barrier along the southern shoreline. This species is found in an area 56 km upstream of the upper falls on the Tahquamenon River (No. 18). The upper Tahquamenon River comes to within 1.6 km of a Lake Michigan stream, the East Branch of the Fox River, tributary to the Manistique River, in which American brook lampreys are abundant.

The four man-made barriers include dams on Pendills Creek (No. 6) and the Betsy (No. 21), Miners (No. 35), and Rock (No. 42) rivers. The dam on Pendills Creek protects 1 km of stream inhabited by American brook lampreys, but 2.4 km downstream of the dam are frequently treated with TFM. Downstream drift of larvae from above the dam rapidly repopulates the lower river after treatments.

All areas containing American brook lampreys in the Betsy River were treated twice before completion of the dam which isolated 22.5 km of larval habitat. The population is slowly rebuilding to previous numbers in this area. The Miners River barrier, installed in 1977 to prevent adult sea lampreys access to a lake in the system, isolated 1.6 km of stream inhabited by American brook lampreys. The Rock River dam, repaired in 1971, has not completely stopped the penetration of sea lampreys. All areas populated by brook lampreys were treated in 1961 and 1971, but a lake within the system provided a recruitment stock of adults to rebuild the population in the area upstream of the lake. Although some adult sea lampreys escaped upstream, since 1971 they have spawned only in the lower section of the stream, and the upper areas have not required treatment.

Canada — Lampricide treatments were conducted on 13 of the 39 streams from which American brook lampreys were collected on the Canadian side. This species was not eradicated from any treated Canadian streams. Natural barriers on 8 of the 13 treated streams restrict sea lamprey distribution. American brook lampreys were collected above natural barriers on four streams: Goulais (No. 12), Chippewa (No. 30), Batchawana (No. 34), and Pancake (No. 38) rivers. Though no collections were made upstream of falls on the Little Carp (No. 4) and Harmony (No. 22) rivers, the abundance of larvae below the falls indicates that this species may also be above these barriers.

American brook lampreys were collected in 26 streams which were never treated, and are abundant in 12 of these (No. 9, 16, 17, 18, 20, 21, 23, 25, 29, 31, 32, and 35). American brook lampreys are abundant not only in many small Canadian streams, but also in many areas of the St. Marys River. Surveys with granular Bayer 73 dislodged as many as 736 larvae from an area of 465 m^2 (Great Lakes Fishery Commission 1973) in the upper river and 522 larvae from a similar area in the lower river.

Ichthyomyzon

DISTRIBUTION AND HABITAT

The lakewide distribution of larvae of the genus *Ichthyomyzon* is described here since no rapid method is available to distinguish Lake Superior species in the larval stage, and since adults were not collected in every stream known to contain ammocoetes. Larval *Ichthyomyzon* were recovered from streams scattered throughout the Lake Superior drainage basin with the exception of the steep, rocky shoreline between the Michipicoten River (No. 41) northwest to the White River (No. 42) in Canada, the Minnesota shoreline in the United States, and the small, cold streams from an unnamed stream (No. 22) to Five Mile Creek (No. 40) in Michigan (Table 1). *Ichthyomyzon* larvae were collected from 105 tributaries of Lake Superior, 59 in the United States (Moore and Braem 1965) and 46 in Canada.

CHANGES IN POPULATION

Ichthyomyzon larvae were distributed over 1299 km in 59 streams (Tables 4 and 5) along the southern shoreline before chemicals were used to control sea lampreys. Nearly 82% (1061 km) of this habitat was treated since 1958 and larvae disappeared from 25 of the treated streams (158 km). *Ichthyomyzon* are found throughout 39 km of habitat above dams, but 102 km of habitat which were never treated could conceivably be invaded by sea lampreys, though this seems less likely now than in the past when sea lamprey adults were much more numerous.

Lampricide applications to eradicate sea lampreys were more harmful to *Ichthyomyzon* species than to American brook lampreys. TFM was applied to 81 (32 in Canada and 49 in the United States) of the 105 streams inhabited by *Ichthyomyzon* larvae, and the genus subsequently disappeared from 41 (16 in Canada and 25 in the United States) of the treated streams. *Ichthyomyzon* larvae are no longer found in five south shore streams (No. 78, 81, 87, 90, and 91) even though lampricide was never applied to them.

Abundance of pretreatment *Ichthyomyzon* populations varied greatly in the streams from which they were later eliminated (Tables 4 and 6). More than 1000 larvae were collected from each of seven streams: No. 38, 42, 56 (Table 6) and No. 18, 44, 51, 54 (Table 4) and more than 100 larvae were reported from another 13 and less than 100 from 21 of the treated streams no longer inhabited by *Ichthyomyzon* larvae.

Ichthyomyzon larvae were readily eliminated from watersheds where they were confined to short stretches and where few sources of recruitment were available. Native larvae disappeared from most streams unless they inhabited areas above barriers, in lentic environ-

TABLE 4. Number of *Ichthyomyzon* larvae and their distribution prior to the disappearance of ammocoetes from 30 United States streams of Lake Superior. (Stream number corresponds to location on Fig. 1. Asterisk indicates stream was not treated.)

Stream number and name	Distribution (km)	Number collected	Years of collections
3 Waiska River	16.1	388	1960–69
6 Pendills Creek	2.4	6	1959–63
18 Tahquamenon River	26.1	1123	1957–71
21 Betsy River	20.7	235	1956–65
44 Chocolay River	21.0	1227	1955–62
45 Carp River	0.4	11	1961–63
51 Salmon Trout River	13.0	2589	1959–63
54 Huron River	11.7	1875	1955–69
58 Falls River	1.1	106	1960–70
59 Six Mile Creek	0.8	1	1962
64 Mud Lake Outlet	1.6	196	1962–71
65 Traverse River	5.1	229	1958–70
68 Eliza Creek	1.1	57	1959–63
69 Gratiot River	0.5	14	1961–63
71 Salmon Trout River	0.8	215	1959–72
72 Elm River	0.4	27	1958–63
74 East Sleeping River	3.5	146	1959–69
78 Second Creek*	0.3	26	1962–63
81 Iron River*	0.2	1	1962
82 Little Iron River	0.4	65	1959–64
83 Union River	0.8	153	1962–64
84 Black River	0.1	1	1963
87 Sioux River*	3.7	1	1963
88 Raspberry River	3.2	8	1962–63
90 Cranberry River*	3.3	29	1959–70
91 Iron River*	2.4	7	1959–67
92 Reefer Creek	1.9	20	1959–64
93 Fish Creek	1.3	174	1961–64
95 Poplar River	8.9	152	1958–70
97 Amnicon River	13.0	309	1958–67
Total	165.8		

TABLE 5. United States tributaries of Lake Superior presently inhabited by *Ichthyomyzon* larvae; original distribution and kilometres of distribution chemically treated. (Stream number corresponds to location on Fig. 1. Asterisk indicates stream was not treated.)

Stream number and name	*Ichthyomyzon* distribution (km)	Distance treated (km)
41 Au Train River	21.0	21.0
43 Laughing Whitefish River	13.0	13.0
47 Dead River*	0.8	0.0
48 Harlow Creek	6.0	6.0
50 Iron River	9.6	3.2
52 Pine River	4.0	2.4
53 Little Huron River*	0.8	0.0
55 Ravine River	8.0	4.8
56 Slate River	1.6	1.6
57 Silver River	4.8	4.8
60 Sturgeon River	163.3	140.0
61 Pike River*	8.0	0.0
62 Pilgrim River	0.8	0.8
63 Trap Rock River	5.6	5.6
66 Tobacco River*	21.7	0.0
67 Little Gratiot River	2.4	2.4
70 Boston-Lily Creek	0.8	0.8
73 Misery River	23.3	19.3
75 Firesteel River	51.5	23.3
76 Flintsteel River*	27.3	0.0
77 Ontonagon River	217.2	214.0
79 Potato River	20.9	20.1
80 Cranberry River	12.9	12.1
85 Bad River	212.3	182.6
86 Fish Creek	29.0	17.7
89 Sand River	4.0	4.0
94 Brule River	85.3	83.7
96 Middle River	33.8	24.1
98 Nemadji River	143.2	98.1
Total	1132.9	905.4

ments, in tributaries in which sea lampreys did not spawn, or in areas difficult to treat such as oxbows, beaver ponds, long estuaries, and springs. *Ichthyomyzon* originally inhabited less than 5 km of stream in 16 of the 25 treated United States streams from which they have disappeared (Table 4).

The presence of barrier falls or dams, and the lack of other sources of recruitment on 19 of the 43 treated streams resulted in efficient treatments and eradication of *Ichthyomyzon*. These streams include 10 (No. 4, 12, 19, 22, 38, 42, 44, 50, 56, and 64) in Canada and 9 (No. 18, 45, 51, 54, 58, 68, 69, 71, and 97) in the United States.

Several treatments over all larval habitat often exterminated *Ichthyomyzon* from a stream. The initial treatments of the Salmon Trout (No. 51) and White (No. 42) rivers nearly eliminated native lampreys. Collections of larval *Ichthyomyzon* in the Salmon Trout River during the treatment years of 1959 and 1963 declined 98% (2482 to 52). This genus accounted for 92% of all lamprey larvae collected in 1959, but only 13% in 1963, and native larvae were never collected after the second treatment. During the initial treatment of the White River in 1963, *Ichthyomyzon* ammocoetes accounted for 94% (4489) of all larvae collected. This genus accounted for 11% (14) of the few larvae (123) collected during a second treatment in 1966. No native lampreys were collected in subsequent treatments.

CURRENT STATUS

United States — *Ichthyomyzon* larvae were found in recent years in 29 south shore tributaries (Table 5). Five of the 29 streams were never treated with TFM including: Dead (No. 47), Little Huron (No. 53), Pike (No. 61), Tobacco (No. 66), and Flintsteel (No. 76) rivers. Few larvae inhabit the Dead and Little Huron rivers, but *Ichthyomyzon* larvae are abundant in 8 km of the Pike, 22 km of the Tobacco, and 27 km of the Flintsteel rivers. Both species of *Ichthyomyzon* inhabited these three streams, and the discovery in

TABLE 6. Number of *Ichthyomyzon* larvae collected during chemical treatments prior to disappearance of ammocoetes from 16 Canadian tributaries. (Stream number corresponds to location on Fig. 1.)

Stream number and name		Number collected
4	Little Carp River	9
5	Big Carp River	40
11	Cranberry River	14
12	Goulais River	501
19	Stokeley River	27
22	Harmony Creek	2
24	Sawmill Creek	2
38	Pancake River	1429
42	White River	4503
44	Little Pic River	2
50	Little Gravel River[a]	43
53	Cash Creek	1
54	Stillwater Creek	126
56	Wolf River	1059
63	Cloud River	27
64	Pigeon River	42

[a] Collected during pretreatment surveys.

1975 of 29 recently transformed silver lampreys in the Tobacco River represents the greatest concentration of this species from any stream in recent years. Why sea lampreys never spawned in these streams is unknown.

Lampricide applications on 24 United States streams presently inhabited by *Ichthyomyzon* larvae greatly decreased the numbers and shortened the distribution of native species. Though *Ichthyomyzon* larvae were recently collected in Harlow (No. 48) and Boston-Lily (No. 70) creeks and the Au Train (No. 41) and Laughing Whitefish (No. 43) rivers, it is doubtful that these stream populations will survive. Downstream drift of sea lampreys into lakes in Harlow and Au Train rivers necessitates annual treatments, and few native larvae are recovered each year. Chemical treatment collections from the Au Train River in 1975, 1976, and 1977 accounted for only 17 *Ichthyomyzon*, and the last larva from Harlow Creek was captured in 1973, although 2847 were collected during the initial treatment in 1959. The 1977 treatment of the Laughing Whitefish River, the second to which all of the *Ichthyomyzon* habitat was exposed, put great stress on this stream population. Native lamprey collections declined from 567 in 1961 to 40 in 1977. The *Ichthyomyzon* population in Boston-Lily Creek appears to be the result of occasional spawning of silver lampreys; only 17 larvae have been collected since 1961.

Ichthyomyzon larvae are uncommon or in danger of disappearing from several streams with existing populations. The Pilgrim (No. 62), Trap Rock (No. 63), and Sand (No. 89) rivers were not treated since lampricide was applied in the early 1960s, yet *Ichthyomyzon* populations never returned to pretreatment levels. Sea lamprey and *Ichthyomyzon* larvae drifted downstream in the Ravine (No. 55), Slate (No. 56), and Silver (No. 57) rivers into Huron Bay where they escaped lampricide applications. While annual treatments of the Huron Bay tributaries since 1973 alleviated the problem of sea lamprey escapement, they eliminated *Ichthyomyzon* species in all Huron Bay tributaries except for 3 km upstream of the chemical application point on the Ravine River.

Ichthyomyzon are abundant in sections of 13 streams, but because of the frequency of treatment, are absent in the lower reaches. Sea lampreys did not penetrate to the upstream distributional limit of *Ichthyomyzon* in these streams, therefore untreated sections that range from less than 1–45 km remain (Table 5). Four treated streams, the Sturgeon (No. 60), Firesteel (No. 75), Bad (No. 85), and Nemadji (No. 98) rivers have more than 16 km of stream that were never treated and presently contain *Ichthyomyzon* larvae. Dams on the Iron (No. 50), Sturgeon, and Bad rivers limited the spread of sea lampreys. *Ichthyomyzon* larvae are distributed throughout the lower 6.4 km of the Yellow Dog River which flows into Lake Independence where a dam at the outlet to the Iron River blocks sea lampreys. *Ichthyomyzon* are also established above a dam on the Sturgeon River for 3 km and a dam on the White River, a tributary of the Bad River, for 30 km. *Ichthyomyzon* larvae are absent from the remaining 183 km of habitat they occupied in the Bad River.

Though no physical barrier exists on several streams, sea lampreys have failed to penetrate into tributaries or through lakes in the system. Untreated areas inhabited by *Ichthyomyzon* above lakes on the Pine (No. 52) and Brule (No. 94) rivers extend 1.6 km on each stream. *Ichthyomyzon* larvae are no longer present in 217 km of the Ontonagon River (No. 77), but still abound in 3 km of a tributary, Mill Creek, above a beaver dam. *Ichthyomyzon* are abundant in 4 km of untreated habitat in the Little Misery River, tributary of the Misery River (No. 73), and in 12 km of the Blackhoof River, tributary of the Namadji River (No. 98). *Ichthyomyzon* also thrive in untreated sections of the East (8 km) and West branches (15 km) of the Firesteel River (No. 75); the South Branch (10 km) of Fish Creek (No. 86); and the Silver (16 km) and Otter (4.8 km) rivers, tributary to the Sturgeon River (No. 60). The upper areas of distribution of *Ichthyomyzon* in the Potato (No. 79, 0.8 km untreated), Cranberry (No. 80, 0.8 km untreated), and Middle (No. 96, 9.7 km untreated) rivers were never penetrated by sea lampreys.

Canada — *Ichthyomyzon* larvae are present in 14 untreated Canadian streams, but they are numerous only in an unnamed stream (No. 46) and Hewitson (No. 47) and Sibley (No. 58) creeks. No *Ichthyomyzon* ammocoetes were collected above waterfalls which are barriers to sea lampreys on the south shore of Lake Superior; however, they are present above four such barrier falls in Canada — on the Big Pic (No. 43), Prairie (No. 45), Gravel (No. 49), and Pearl (No.

57) rivers, and also above a dam on the Black Sturgeon River (No. 55). Abundance and distribution of native lampreys upstream of these barriers were not determined. Offshore populations of *Ichthyomyzon* larvae in Batchawana Bay provide limited recruitment to streams in the area, but frequent stream treatments have greatly reduced these populations. Five other treated streams (No. 48, 51, 52, 60, and 61) contain viable populations of *Ichthyomyzon* in Canada.

Northern Brook Lampreys

DISTRIBUTION AND HABITAT

Distribution of the two species of *Ichthyomyzon* along the southern shoreline of Lake Superior was determined from adult collections. Northern brook lampreys were found in 35 United States streams — 24 previously described (Moore and Braem 1965) and 11 additional streams (No. 41, 43, 47, 56, 62, 63, 77, 79, 80, 86, and 89). Unfortunately, well-documented stream distribution for silver lampreys and northern brook lampreys is not available for Canadian streams. Northern brook lampreys were most common in medium-to-large streams with average summer flows of 0.3 to 28.3 m^3/s. This species was common in several turbid streams. Streams inhabited by northern brook lampreys along the western half of the United States shoreline were generally warmer than eastern streams inhabited by American brook lampreys.

CURRENT STATUS

Northern brook lampreys are presently more common than silver lampreys in the Lake Superior drainage basin. They were collected in 35 United States tributaries, and *Ichthyomyzon* larvae are still present in 27 of the 35 streams. Since 1973, adult northern brook lampreys were collected from 22 of the 29 streams which presently contain *Ichthyomyzon* larvae (Table 1).

Silver lampreys were uncommon in Canadian streams before lampricide applications, and we assume that most *Ichthyomyzon* larvae recently collected were northern brook lampreys. Since adult *Ichthyomyzon* have not been identified to species in Canada in recent years, detailed distribution is not possible; however, *Ichthyomyzon* larvae above barriers are probably northern brook lampreys.

Silver Lampreys

DISTRIBUTION AND HABITAT

The original distribution and abundance of silver lampreys were determined from catches at electric barriers. Since 1959 accurate counts of this species were kept at all barriers. Silver lampreys were considered plentiful along the southern shoreline (2000 or more captured in one season at all United States barriers), but not taken in great numbers from any one stream (McLain et al. 1965).

Silver lampreys were widely dispersed along the Lake Superior shoreline, but were most abundant in a few zones and streams (Table 1). A total of 4278 silver lampreys were captured from 35 of 55 barriers which were operated in 1959. Most silver lampreys were captured at barriers in the southwestern portion of the lake: 92% (3925) were captured in streams from the eastern tip of the Keweenaw Peninsula to the Minnesota and Wisconsin border. The effects of the six previous seasons of barrier operation and of sea lamprey competition with the silver lamprey population of Lake Superior are unknown.

Few silver lampreys were collected from Canadian electric barriers; the maximum number of silver lampreys for 1 yr, 97, was collected in 1956. Both parasitic lampreys were scarce in Canada in 1959 — less than 1% of the silver lampreys and 4% of the sea lampreys captured at Lake Superior barriers in 1959 were collected in Canada. Though silver lampreys were rarely observed in recent years along the Canadian shoreline, commercial fishermen reported that they were common near Thunder Bay at the turn of the century (Allin 1951).

Silver lampreys apparently require more specialized conditions than sea lampreys for successful spawning and their larvae may be less competitive than American brook larvae. This species was scarce in most streams along the southeastern shoreline, where American brook and sea lampreys abound. Silver lampreys were also rarely associated with American brook lampreys in Lower Michigan (Morman 1979). A total of 95% of the 1959 catch (4058) was taken in 12 streams, including only the Waiska River (No. 3) in the eastern half of the lake (Table 7). The Sturgeon River (No. 60), one of the largest tributaries of Lake Superior with 174 km of main stream (Brown 1944) and average summer flow of 28.3 m^3/s (Smith et al. 1974), accounted for 45% (1913) of the entire catch.

Silver lampreys were distributed throughout the Lake Superior drainage basin. They were collected from 42 United States streams, 35 described by Moore and Braem (1965) and 7 (No. 28, 49, 58, 62, 66, 70, and 71) recently documented. Eddy and Underhill (1943) reported specimens were previously taken in the St. Louis River (No. 99), but none were collected since sea lamprey control was initiated. Silver lampreys were observed in 19 streams (No. 4, 5, 11, 12, 19, 22, 30, 34, 36, 38, 40, 41, 42, 45, 48, 58, 60, 61, and 63) along the north shore of Lake Superior. *Ichthyomyzon* larvae in the Prairie (No. 45) and Pays Plat (No. 48) rivers were identified as silver lampreys (V. D. Vladykov et al., Department of Lands and Forests, Ont., Canada, 1953, unpublished data).

Silver lampreys were collected in Lake Superior streams with average summer flow as low as 0.03 m^3/s, but average summer flows in the 12 streams which accounted for 95% of the 1959 silver lamprey catch ranged from 0.4 to 28 m^3/s. This species inhabited several turbid streams and often was found in rivers associated with bays.

TABLE 7. Number of silver lampreys taken at 12 electric barriers operated in tributaries of Lake Superior, 1959–70. (Stream number corresponds to location on Fig. 1. Dash indicates that barrier was not in operation. Chemical treatment years are designated by an asterisk.)

Stream number and name	Flow (m^3/s)	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970
3 Waiska River	0.8	161	281*	296	8	3	7*	—	—	—	—	—	—
60 Sturgeon River	28.0	1913	416*	297	59	96*	225	22	159*	68*	75	32*	110*
65 Traverse River	1.1	65*	—	—	—	—	—	—	—	—	—	—	—
67 Little Gratiot River	2.1	64*	—	—	—	—	—	—	—	—	—	—	—
73 Misery River	1.7	186*	75	105	15	5*	13	2	7	3	0	3	3
75 Firesteel	1.7	215*	131	383	20	22	14*	11	7	8	8	4	8
85 Bad River	19.6	90	—	—	—	—	—	—	—	—	—	—	—
86 Fish Creek	2.4	103*	23	—	—	—	—	—	—	—	—	—	—
94 Brule River	5.9	633	149	254	137*	77	25	25*	11	11	16	0*	8
95 Poplar River[a]	0.4	106	52	117	9*	—	—	—	—	—	—	—	—
96 Middle River[a]	0.6	376	176	482	150*	361	12	12	3	2	1	2	3
97 Amnicon River[a]	1.4	146	111	182	72*	309	4	7	5	2*	3	4	7
Total		4058	1414	2116	470	873	300	79	192	94	103	45	139

[a] Treated in 1958.

CHANGES IN POPULATION

Chemical control of sea lampreys caused a sharp decline in the silver lamprey population of Lake Superior. Lampricide applications to large streams, especially in the southwestern part of the drainage basin, noticeably decreased barrier collections of silver lampreys. The 1959 barrier collections reflect the pretreatment distribution and abundance of silver lampreys (Table 1). Though the first field applications of selective lampricides were made during the summer of 1958 (Applegate et al. 1961), the effects of the first round of chemical treatments were not realized at electric barriers for 2 yr. Because of the silver lamprey's parasitic life cycle, recruitment to stream populations was available from the year-class feeding in the lake which was unaffected by lampricide applications.

Barrier collections from the Waiska River (No. 3) near Sault Ste. Marie, Michigan, clearly demonstrate the results of an effective TFM treatment upon a stream population of silver lampreys. The barrier catch of silver lampreys in 1960 just before treatment totaled 281 lampreys; the catch increased slightly to 296 in 1961. The effects of treatment were apparent in 1962 when the spawning run declined to eight adults, a 97% reduction. The 1960 treatment effectively eliminated this species from the Waiska River.

One treatment did not always eliminate silver lampreys from a river, but several treatments of major rivers in each portion of the drainage basin decreased barrier catches by over 90% (Table 7). Although the Sturgeon River (No. 60) was treated more frequently than the other streams from 1959 to 1970, silver lampreys were not eradicated. Many oxbows and a lake within the system created treatment problems which were partially solved by refinement of methods and equipment. Since sea lampreys never penetrated as far as the known distribution of *Ichthyomyzon* larvae, all areas inhabited by silver lampreys may not have been treated. The 110 silver lampreys collected in 1970, however, did represent a 94% decrease from the 1959 catch, and indicated that this species has been most prevalent in the treated portion of the river.

The decline of silver lampreys in the Misery (No. 73) and Firesteel (No. 75) rivers was not evident until 1962 when the total catch declined 91% over the 1959 catch. The extra year to attain control may reflect a 1960 treatment of a large nearby river, the Ontonagon River (No. 77, 19.8 m^3/s). Many *Ichthyomyzon* larvae and several recently transformed adult silver lampreys were recovered during the 1960 treatment of the Ontonagon River.

Several treatments of all major rivers in Wisconsin greatly reduced silver lamprey collections at electric barriers. The combined effects of the 1958 and 1962 treatments of the Brule (No. 94), Middle (No. 96), and Amnicon (No. 97) rivers were evident in the 1964 barrier catch of 41 silver lampreys, a 96% decline from the 1959 catch (1155).

The barrier network was gradually reduced after the development of TFM for sea lamprey control. Sixteen index barriers were operated along the southern shoreline through 1970, following which eight barriers were operated to assess adult sea lamprey populations and evaluate chemical control. Eight barriers were operated in Canada from 1961 to 1967, when the program was terminated.

CURRENT STATUS

Few silver lampreys were reported in Lake Superior tributaries from 1973 to 1977. No *Ichthyomyzon* larvae were recently recovered from 21 of the 42 United States streams from which silver lampreys were reported, and this species was collected in just 9 of the 29 United States streams which presently contain *Ichthyomyzon* larvae. Since 1970, eight barriers were operated on Lake Superior, and 45 silver lampreys were collected from the Silver (No. 57), Brule (No. 94), and Amnicon (No. 97) rivers — 16 in the last 5 yr. *Ichthyomyzon* larvae were not recovered from the Amnicon River since 1966. Silver lampreys were recovered during surveys of six Lake Superior tributaries and the St. Marys River from 1973 to 1978. The streams and number of adult silver lampreys include Sturgeon (No. 60, 4), Pilgrim (No. 62, 1), Little Gratiot (No. 67, 15), Misery (No. 73, 1), and Tobacco (No. 66, 29) rivers and Fish Creek (No. 86, 21), and the St. Marys River (4).

Vulnerability of Native Species to Chemical Control

Vulnerability of native lampreys to lampricide applications is dependent upon distribution of each species in relation to that of the sea lamprey. The sea lamprey probably spread throughout the lake by attachment to fish and vessels and by reproducing in a wide range of stream environments, but the habitats and habitat requirements of native lampreys restricted their distribution within the Lake Superior drainage basin and within individual streams. Because the Chocolay River (No. 44) represents several rivers with more than one native lamprey species present, and the changes in numbers and distribution resulting from sea lamprey control measures are well documented, the progression of events in this stream can be used to illustrate the effects on endemic species and suggest reasons for differential vulnerability of nonparasitic species.

LAMPREYS IN THE CHOCOLAY RIVER

The Chocolay River is one of 22 tributaries of Lake Superior that contains three genera of lampreys, including four species: American brook, northern brook, sea, and silver lampreys. Only three silver lampreys were collected at the electric barrier from 1951 to 1978, and the absence of transformed silver lampreys in collections of 1220 *Ichthyomyzon* larvae strongly suggests that all ammocoetes of the genus examined are northern brook lampreys. *Ichthyomyzon* larvae will thus be referred to in this section as northern brook lampreys. Pretreatment distribution of native lampreys in the Chocolay River was determined from collections of ammocoetes during the original treatment of the main stream in 1958.

A low barrier falls 33 km upstream of the Chocolay River mouth limits lamprey distribution (Fig. 2). American brook and northern brook lampreys were distributed from the mouth upstream 22 and 21 km, respectively. Sea lampreys were dispersed through the entire 33 km, and by 1958, the population in the area below the falls was the largest of any encountered in a Michigan tributary of Lake Superior (Stauffer and Hansen 1958).

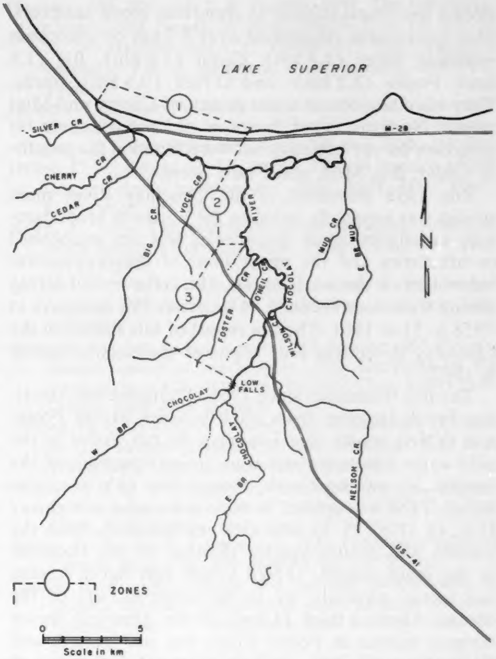

FIG. 2. Chocolay River system, Lake Superior, showing locations of tributaries and the three zones in which lampreys were collected.

Sea lamprey larvae predominated (65–100% of all lampreys collected) in all samples taken from the main stream in 1958 (Table 8). Most nonparasitic lampreys were collected in the middle section of the main stream (58% of all American brook and 63% of all northern brook lampreys). The small, cold tributaries to the main

TABLE 8. Number and percentage (in parentheses) of three species of lampreys collected from various zones in the Chocolay River during 1968. (Location of zones are shown in Fig. 2.)

Zone	Distance upstream of mouth (km)	Number of lampreys collected			
		Sea	American brook	Northern brook	Total
1	0–12	767 (65)	157 (13)	264 (22)	1188 (100)
2	12–20	1734 (73)	213 (9)	442 (18)	2389 (100)
3	20–33	681 (100)	0	0	681 (100)
Total		3182	370	706	4258

stream were most suitable to American brook lampreys. This species was established over 8.7 km of tributaries including Silver (1.8 km), Cedar (1.6 km), Big (1.8 km), Foster (3.2 km), and O'Neil (0.3 km) creeks. They were also found at the mouth of Cherry and Mud creeks. Northern brook lampreys did not penetrate far upstream on any tributary but were found at the mouths of Cedar, Big, Mud, and Foster creeks.

The 1958 treatment of the Chocolay River main stream was especially lethal to the northern brook lamprey population since this species was not established in tributaries and the upper limit of distribution was below that of the sea lamprey. The collection of larvae during treatment declined 96%, from 706 lampreys in 1958 to 31 in 1961. The last report of this species in the Chocolay River was four adults at the electric barrier in 1962.

The five treatments since 1958 eliminated the American brook lamprey from all tributaries except Foster and O'Neil creeks. Sea lampreys do not thrive in the cold-water tributaries and were found upstream of the mouth only in Big Creek, though few (8) were collected. TFM was applied to these tributaries at highway U.S. 41 (Fig. 2) to eliminate sea lampreys from the mouths and ensure against dilution of the chemical in the main stream. O'Neil Creek was never treated and larvae currently are in the lower 0.3 km of the stream. About a third (1 km) of the American brook lamprey habitat in Foster Creek was not treated, and larvae from this area drifted into treated portions of the Chocolay River. The number of larvae decreased considerably in Foster Creek. Surveys in 1956 at highway U.S. 41 and the mouth accounted for 132 and 126 larvae per hour of collecting. Surveys at similar stations in 1976 recovered 45 larvae per hour at highway U.S. 41 and 11 larvae per hour at the mouth.

Chemical treatments altered the species composition of lampreys in the Chocolay River. Several treatments over areas inhabited by nonparasitic lampreys effectively eliminated both species. Northern brook lampreys were eradicated from 21 km of the main stream, and American brook lampreys from Big, Cedar, and Silver creeks and much of the main stream, but are still present in Foster and O'Neil creeks. Sea lamprey larvae have not been collected in the Chocolay River since 1973. Changes in nonparasitic lamprey populations in the Chocolay River reflect, in general, the results in other Lake Superior tributaries.

FACTORS AFFECTING SURVIVAL

As demonstrated in the Chocolay River, the location of larval populations within a stream, especially in relation to the upstream distribution of sea lamprey ammocoetes, determines species survival through lampricide applications. Brook lampreys predominate in the higher reaches and parasitic species predominate in the lower reaches of streams (Hardisty and Potter 1971). In Lake Superior streams the parasitic sea lampreys often migrated upstream beyond the limits of nonparasitic lampreys.

Sea lampreys migrated beyond the upstream limit of silver lampreys in all Lake Superior streams inhabited by both species. Silver lampreys preferred the lower sections of large streams tributary to Lake Huron (Morman 1979) and were found in lower portions of large tributaries in Illinois (Smith 1965). Restriction of silver lampreys to a relatively short stretch of river downstream of sea lamprey larvae would increase vulnerability to treatment, since their entire distribution would be exposed to the effects of the lampricide.

Fecundity of a species is important in the recovery of that species after treatments. Populations from different localities exhibit a wide variability in fecundity (Kott 1971). The absolute fecundity of parasitic lampreys, however, is greater than nonparasitic lampreys. Fecundity of silver lampreys (19 012 eggs) was found to be nearly 12 times greater than that of northern brook lampreys (1524 eggs) and 8 times greater than that of American brook lampreys (2339 eggs) in Quebec (Vladykov 1951). The fecundity of all native lampreys is overshadowed by sea lampreys (68 599 eggs) in Lake Superior (Manion 1972).

The silver lamprey's greater fecundity and mobility due to a parasitic phase suggest that it would be less vulnerable to chemical treatment than would nonparasitic lampreys. Recent scarcity of this species in Lake Superior, however, indicates that other factors have limited its survival.

The advantages of greater fecundity and mobility shared with the sea lampreys were negated by the more stringent spawning requirements of this species. Nearly all (95%) silver lampreys captured at barriers in 1959 were taken from just 12 streams. The collection of nine sea lampreys, on the average, for each silver lamprey from these 12 streams in 1959 indicates that before chemical control, the invading sea lamprey had already established a competitive advantage in Lake Superior. Silver lampreys were previously unable to compete with this invader and disappeared from Lake Ontario and the Finger Lakes of New York (Hubbs and Trautman 1937). Treatment of the 12 streams from which 95% of the silver lampreys were collected in 1959 sharply decreased catches of this species at electric barriers.

The highly adaptable sea lamprey reproduced in streams suitable to each of the native lampreys. Sea lampreys invaded 77% (81 of 105) of the *Ichthyomyzon* streams and 48% (42 of 88) of the American brook streams. Subsequent treatments eliminated *Ichthyomyzon* from 51% (41 of 81) of these streams, but American brook lampreys have disappeared from 14% (6 of 42). In United States streams, however, nearly equal portions of the total *Ichthyomyzon* and American brook lamprey distribution (kilometres of stream) were treated, 82 and 83%, respectively.

Distribution of American brook lampreys within Lake Superior tributaries contributed to their recovery after chemical treatments. This species inhabits some small, cold streams and tributaries rarely inhabited by sea lampreys, and is more likely to establish in headwaters upstream from sea lamprey distribution. American brook larvae are also more common in lacustrine environments.

Concern over the loss of nonparasitic lampreys, especially American brook lampreys in Great Lakes tributaries, was expressed by Vladykov (1973). Lampricide applications have, however, caused a greater decrease in numbers and distribution of northern brook and silver lampreys than American brook lampreys in Lake Superior streams. *Ichthyomyzon* species have been eliminated from more streams and are less likely to recover from a single chemical treatment of all suitable habitat.

The Great Lakes Fishery Commission and their two agents, the United States Fish and Wildlife Service and the Department of Fisheries and Oceans of Canada, are committed to a program of integrated control which will use all suitable techniques for sea lamprey control. As other methods, including barrier dams, are developed and implemented, the use of lampricides will decrease and therefore the impact of the program on native species will diminish.

Acknowledgments

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ALLIN, A. E. 1951. Records of the sea lamprey and the silver lamprey from the Canadian waters of the western end of Lake Superior. Can. Field-Nat. 65: 184–185.

APPLEGATE, V. C., J. H. HOWELL, J. W. MOFFETT, B. G. H. JOHNSON, AND M. A. SMITH. 1961. Use of 3-trifluormethyl-4-nitrophenol as a selective sea lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 1: 35 p.

BRAEM, R. A., AND W. J. EBEL. 1961. A back-pack shocker for collecting lamprey ammocetes. Prog. Fish-Cult. 23: 87–91.

BROWN, C. J. D. 1944. Michigan streams — their lengths, distribution, and drainage areas. Mich. Dep. Conserv. Inst. Fish Res. Misc. Pub. 1: 21 p.

DAVIS, W. A. 1970. The comparative susceptibility of three genera of larval lampreys to a lampricide. Univ. Guelph, M.S. thesis, Guelph, Ont. 52 p.

DAWSON, V. K., K. B. CUMMING, AND P. A. GILDERHUS. 1975. Laboratory efficacy of 3-trifluoromethyl-4-nitrophenol (TFM) as a lampricide. U.S. Fish Wildl. Serv. Invest. Fish Control 63: 10 p.

EDDY, S., AND J. C. UNDERHILL. 1943. Northern fishes. Univ. Minnesota Press, Minneapolis. 414 p.

GREAT LAKES FISHERY COMMISSION. 1973. Annual Report of the Great Lakes Fishery Commission, Ann Arbor, MI. p. 51.

HARDISTY, M. W., AND I. C. POTTER. 1971. The behaviour, ecology, and growth of larval lampreys, p. 85–125. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London and New York.

HOWELL, J. H., AND W. M. MARQUETTE. 1962. Use of mobile bioassay equipment in the chemical control of sea lamprey. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 418: 9 p.

HUBBS, C. L., AND M. B. TRAUTMAN. 1937. A revision of the lamprey genus *Ichthyomyzon*. Misc. Publ. Mus. Zool., Univ. Mich. 35: 109 p.

KOTT, E. 1971. Characteristics of pre-spawning American brook lampreys from Big Creek, Ontario. Can. Field-Nat. 85: 235–240.

MANION, P. J. 1972. Fecundity of sea lamprey (*Petromyzon marinus*) in Lake Superior. Trans. Am. Fish. Soc. 101: 718–720.

MCLAIN, A. L., B. R. SMITH, AND H. H. MOORE. 1965. Experimental control of sea lampreys with electricity on the south shore of Lake Superior, 1953–60. Great Lakes Fish. Comm. Tech. Rep. 10: 48 p.

MOORE, H. H., AND R. A. BRAEM. 1965. Distribution of fishes in U.S. streams tributary to Lake Superior. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 516: 61 p.

MORMAN, R. H. 1979. Distribution and ecology of lampreys in the Lower Peninsula of Michigan, 1957–75. Great Lakes Fish. Comm. Tech. Rep. 33: 59 p.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

SMITH, B. R. 1962. Spring and summer temperatures of streams tributary to the south shore of Lake Superior, 1950–60. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. 410: 57 p.

SMITH, B. R., AND A. L. MCLAIN. 1962. Estimation of the brook and sea lamprey ammocete populations of three streams. Great Lakes Fish. Comm. Tech. Rep. 4: 26 p.

SMITH, B. R., J. J. TIBBLES, AND B. G. H. JOHNSON. 1974. Control of the sea lamprey (*Petromyzon marinus*) in Lake Superior, 1953–70. Great Lakes Fish. Comm. Tech. Rep. 26: 60 p.

SMITH, P. W. 1965. A preliminary annotated list of the lampreys and fishes of Illinois. Ill. Nat. Hist. Surv. Biol. Notes 54: 12 p.

STAUFFER, T. M., AND M. J. HANSEN. 1958. Distribution of sea lamprey ammocetes in Michigan tributaries of Lake Superior, 1955–57. Mich. Dep. Conserv. Inst. Fish. Res. Misc. Pub. 11: 25 p.

STERBA, G. 1962. Die Neunaugen (Petromyzonidae). Handb. Binnenfischerei Mitteleuropas 38(10): 132–133. (Transl. from the German by R. W. McCauley, 138 p.)

TIBBLES, J. J. 1961. Preparations for lamprey control in Lake Huron. Fish. Res. Board Can. Prog. Rep. Biol. Sta. Tech. Unit (London, Ont.) 1: 22–27.

U.S. DEPARTMENT OF COMMERCE. 1974. Great Lakes Pilot. National Oceanic and Atmospheric Administration, Detroit, MI. p. 555.

VLADYKOV, V. D. 1951. Fecundity of Quebec lampreys. Can. Fish. Cult. 10: 1–14.

1973. North American nonparasitic lampreys of the family Petromyzonidae must be protected. Can. Field-Nat. 87: 235–239.

WAGNER, W. C., AND T. M. STAUFFER. 1962. The population of sea lamprey larvae in East Bay, Alger County, Michigan. Pap. Mich. Acad. Sci. Arts Lett. 47: 235–245.

Effects of Control of the Sea Lamprey (*Petromyzon marinus*) on Migratory and Resident Fish Populations[1]

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Information from the records of the various agencies on control of the sea lamprey (*Petromyzon marinus*) was summarized from the early approach to control by mechanical or electrical barriers and chemical toxicants. While fish kill has been an inescapable consequence of the program, information available for migratory species has shown no large-scale detrimental effects. The only reportable instance of damage to a resident stream species has been the near loss of the stonecat (*Noturus flavus*) from tributaries to the southwest corner of Lake Superior, resulting from chemical treatments. Although no similar occurrences were recognized, available documentation proved inadequate to record long-term effects on these vulnerable species. As long as existing control methods continue, no matter the precautions taken, fish populations will be affected. Whether or not this remains a tenable situation is a question for this symposium and the future.

Key words: weirs, chemicals, fish kills, sea lamprey, *Petromyzon marinus; Catostomus catostomus, Catostomus commersoni, Noturus flavus, Salvelinus fontinalis*

DAHL, F. H., AND R. B. MCDONALD. 1980. Effects of control of the sea lamprey (*Petromyzon marinus*) on migratory and resident fish populations. Can. J. Fish. Aquat. Sci. 37: 1886–1894.

On trouvera ici un résumé de l'information recueillie à même les dossiers de divers organismes sur le contrôle de la grande lamproie marine (*Petromyzon marinus*) depuis les débuts jusqu'au contrôle par barrières mécaniques ou électriques et substances chimiques toxiques. Une des conséquences inévitables du programme a été des mortalités de poissons. Cependant, les renseignements dont on dispose sur les espèces migratrices n'indiquent pas d'effets nuisables de grande envergure. Le seul cas digne de mention de dommage à une espèce résidant dans les cours d'eau a été la quasi-disparition de la barbotte des rapides (*Noturus flavus*) des tributaries du coin sud-ouest du lac Supérieur, à la suite de traitements chimiques. Bien que d'autres cas semblables n'aient pas été reconnus, la documentation disponible ne suffit pas à démontrer des effets à long terme sur ces espèces vulnérables. Les populations de poissons seront affectées tant que se poursuivront les méthodes de contrôle actuelles, quelles que soient les précautions prises. C'est au présent colloque et à l'avenir de décider si cette position est défendable ou non.

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ATTEMPTS to control sea lamprey (*Petromyzon marinus*) in the Great Lakes began in 1950 with the installation of mechanical weirs and traps in northern Lake Huron and a weir on Pendills Creek, Lake Superior (Applegate and Smith 1950). Within 3 yr, electromechanical weirs or barriers were developed and placed in operation in 10 eastern Lake Superior streams (Applegate et al. 1952b). Weirs were installed progressively from east to west in tributaries on the Canadian and United States shorelines of Lake Superior until, by 1957, the network extended to Thunder Bay, Ontario, and Superior, Wisconsin (Erkkila et al. 1956; Lenson and Lawrie 1959; McLain et al. 1965). Extension of the barrier network into Lakes Michigan and Huron began in 1954, and eventually 182 tributaries of the upper three lakes had control structures installed for one or more years.

Refinements of, and improvements to, the electrical barriers were an ongoing process. As time and finances permitted, abutments were built, traps were improved, and some weirs were moved to new and better loca-

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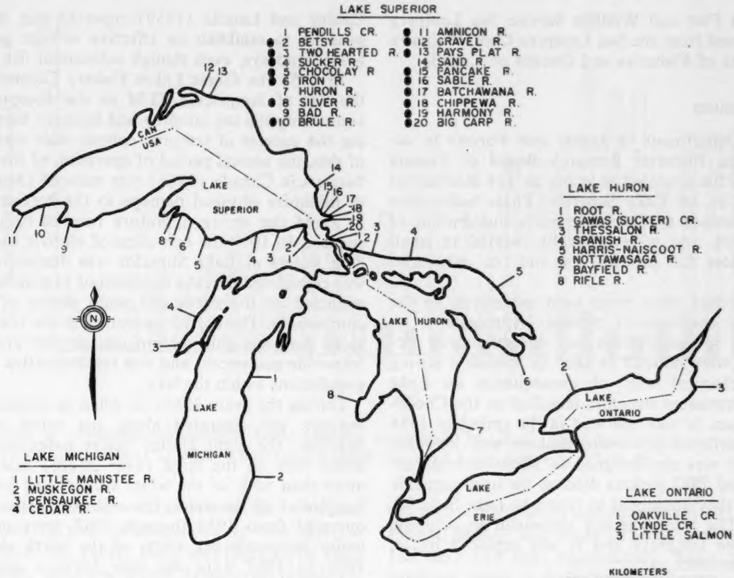
LAKE SUPERIOR
● 1 PENDILLS CR.
● 2 BETSY R.
● 3 TWO HEARTED R.
● 4 SUCKER R.
● 5 CHOCOLAY R
● 6 IRON R.
7 HURON R.
● 8 SILVER R.
9 BAD R.
●10 BRULE R.
● 11 AMNICON R.
● 12 GRAVEL R.
● 13 PAYS PLAT R.
14 SAND R.
● 15 PANCAKE R.
● 16 SABLE R.
● 17 BATCHAWANA R.
● 18 CHIPPEWA R.
● 19 HARMONY R.
●20 BIG CARP R.
LAKE HURON
1 ROOT R.
2 GAWAS (SUCKER) CR.
3 THESSALON R.
4 SPANISH R.
5 HARRIS-NAISCOOT R.
6 NOTTAWASAGA R.
7 BAYFIELD R.
8 RIFLE R.
LAKE MICHIGAN
1 LITTLE MANISTEE R.
2 MUSKEGON R.
3 PENSAUKEE R.
4 CEDAR R.
LAKE ONTARIO
1 OAKVILLE CR.
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CAN
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FIG. 1. Location of streams where 16 weirs were operated on Lake Superior (dots), and tributaries of the Great Lakes with significant fish kills as a result of the sea lamprey control program.

tions to reduce fish mortality. Experimentation with direct-current weirs between 1952 and 1956 culminated in the development of a direct-current diversion device to lower fish mortality on problem streams (McLain and Nielsen 1953; McLain 1957).

A chemical screening program conducted at the Hammond Bay Laboratory between 1953 and 1956 resulted in the discovery of 3-trifluoromethyl-4-nitrophenol (TFM), which is toxic to lamprey ammocoetes and relatively harmless to fish (Applegate et al. 1957). Field testing of this chemical was conducted in the spring and summer of 1958 (Applegate et al. 1961), and full-scale application to known sea lamprey producing streams began in the fall of that year. Further refinements to the lampricide were made when it was discovered that the addition of a small percentage of 2′,5-dichloro-4′-nitrosalicylanilide (Bayer 73) to TFM maintained the selective toxicity, but lowered the amount of TFM required to treat streams (Howell et al. 1964).

Each of the methods of sea lamprey control had, to a varying degree, effects on resident fish stocks and migratory species which used the streams for spawning. Although control operations were widespread, major problems were on a limited number of streams on the Great Lakes (Fig. 1). The effects of sea lamprey weirs and chemical treatments on fishes, particularly rainbow trout (*Salmo gairdneri*), longnose sucker (*Catostomus catostomus*), white sucker (*C. commersoni*), stonecat (*Noturus flavus*), and brook trout (*Salvelinus fontinalis*) in tributary streams of lakes Superior, Michigan, Huron, and Ontario are described in this paper. The five species were selected as representative of special problems associated with sea lamprey control.

Materials and Methods

Fish catch and mortality data for Lake Superior were collected from eight electric barriers along the south shore from 1958 through 1979, and fish mortality data from eight weirs operated along the Canadian shoreline between 1956 and 1967. While earlier data are provided for the south shore barriers, consistency between annual fish catches occurred only upon completion of the direct-current guider network in 1958. The United States weirs included the Betsy, Two Hearted, Sucker, Chocolay, Iron, Silver, Brule, and Amnicon rivers; and the Canadian weirs included the Gravel, Pays Plat, Pancake, Sable, Batchawana, Chippewa, Harmony, and Big Carp rivers (Fig. 1). These records were examined to determine the effects of the weirs, as well as long-term effects of chemical treatments, on fish stocks.

The extent of fish mortality in tributaries of Lakes Michigan and Huron was obtained from data gathered at 49 weirs along the north shore of Lake Michigan and 12 weirs along the north and east shores of Lake Huron.

Data on fish mortality, attributable to chemical treatment of streams and bays tributary to Lakes Superior, Michigan, Huron, and Ontario, were compiled from records of the United States Fish and Wildlife Service Sea Lamprey Control Stations and from the Sea Lamprey Control Centre of the Department of Fisheries and Oceans of Canada.

MECHANICAL BARRIERS

The Ontario Department of Lands and Forests in cooperation with the Fisheries Research Board of Canada during the mid-1950s operated as many as 114 mechanical check weirs, in 1 yr, on Lake Superior. These weirs were used as survey devices to determine early distribution of adult sea lampreys, and were generally located in small tributaries with low fish productivity and for only brief periods of time.

Mechanical barriers were never used extensively in the United States for sea lamprey control (Applegate et al. 1952a). The cost of construction and operation was prohibitive and they were difficult to keep in operation during floods. One mechanical weir of consequence on Lake Superior was a permanent structure installed on the Chocolay River, Michigan. It was operated in the spring of 1954 and captured nearly 30 000 white suckers and longnose suckers. The weir was not designed to allow downstream passage of fish, and 7887 suckers died on the upstream side of the weir when they attempted to return to Lake Superior after spawning. The weir was not successful in stopping the passage of sea lampreys and it was replaced by an electrical barrier in 1955.

ELECTRICAL BARRIERS

The alternating-current barrier operation, as initiated in Lake Superior for sea lamprey control, is well documented by McLain et al. (1956), Smith (1971), and Smith et al. (1974). The electromechanical weirs that were operated in the United States from 1953 to 1955 were not designed for attracting and trapping fish, which resulted in a relatively high mortality. Some of the weirs were built in unsuitable areas to be located below sea lamprey spawning grounds. Location of barriers where stream flows were slow or subject to reversal because of lake seiche and poor placement of traps were the major causes of fish mortality (Erkkila et al. 1956).

The installation of direct-current diversion devices on two United States streams in 1956 was a successful attempt in attracting and trapping fish to reduce fish mortality in problem streams (McLain 1957). The addition of these devices to five of the eight United States index weirs was completed in 1958, and the weirs have been operated in essentially the same manner through 1979.

Although early Canadian weir designs on Lake Superior incorporated traps, initially within the electrical barrier array (which were found to disrupt the electrical field) and subsequently down or upstream of the more efficient bank-to-bank barriers, they were ineffective in live-trapping fish. The Canadian barriers were gradually developed into blocking weirs with nets of wire mesh or chain link stretched across the river below, and where necessary above, the barriers to prevent fish from penetrating the electrical field (Lenson and Lawrie 1959). By 1962 the nets were abandoned, after repeated efforts to improve their effectiveness had failed. No further attempts were made to divert or entrap fish approaching the index barriers. Direct-current guider devices were not installed in Canada, partly because of an unsuccessful effort to develop a direct-current guider-barrier on the Thessalon River, Lake Huron, in 1959. McCauley and Loucks (1959) reported that it had not been possible to establish an effective voltage gradient to stop adult lampreys, even though substantial fish kills occurred.

In 1959 the Great Lakes Fishery Commission endorsed the use of lampricide TFM as the accepted method for controlling the sea lamprey and lamprey barriers for assessing the success of lamprey control with toxicants. Because of this, the annual period of operation of the Lake Superior barriers in Canada (1961) was reduced (May 15–June 30) to minimize physical damage to the barriers by flood and to avoid the spring migratory runs of rainbow trout and suckers. In 1967 the operation of electric barriers in Canadian waters of Lake Superior was discontinued because it was considered that the fluctuations in numbers of lampreys collected on the north and south shores of the lake were comparable. The barrier operation in the United States provided sufficient information on lamprey and fish runs for lake-wide assessment and was representative of sea lamprey populations within the lake.

During the years 1958–70, when an extensive network of barriers was operated along the south shore of Lake Superior, the eight United States index weirs trapped or killed 30% of the large (over 30 cm) rainbow trout and more than 50% of the white suckers and longnose suckers handled at all the weirs. The eight Canadian index barriers, operated from 1956 through 1967, were on some of the major fish-producing rivers of the north shore, and from 1961 to 1967 were the only barriers operating on the Canadian side of Lake Superior. The index barrier records are thus highly indicative of the effects on fish of the entire barrier network of Lake Superior.

Lake Superior received the highest priority for lamprey barrier operations in the 1950s and weirs were installed in Lakes Michigan and Huron when funds and manpower were available. Consistency in data collection at that time was not a coansideration. While a long-term data base is thus unavailable from Lakes Michigan and Huron, some relevant barrier data have been used to supplement the Lake Superior information.

CHEMICAL CONTROL

Information of the effects of toxicants used to control the sea lamprey on fish is derived from objective assessments made by treatment personnel during, and occasionally subsequent to, the course of treatment.

Effects of Sea Lamprey Weirs on Fishes

Rainbow trout were introduced into the upper Great Lakes in the late 1800s. They adapted readily and soon became a favorite trophy fish for sportsmen. Prior to sea lamprey control, the records of migratory rainbow trout were fragmentary. Creel censuses by conservation officers of the various State departments of Natural Resources were conducted on a "time available" basis and varied greatly from area to area. As there was no differentiation between large and small fish of the species, it was difficult to determine the numbers of migratory rainbow trout from Great Lakes waters. The number of migratory rainbow trout collected at the electrical barriers was never large.

White suckers and longnose suckers were never commercially exploited (Baldwin and Saalfeld 1962) and

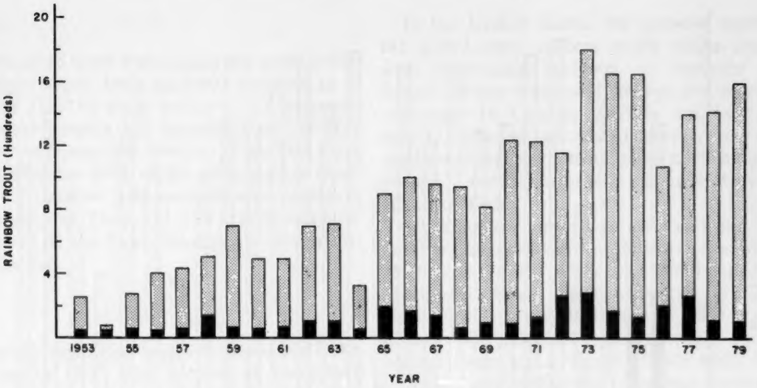

FIG. 2. Number of rainbow trout (*Salmo gairdneri*) handled (open bars) and number killed (solid bars) at eight weirs on the south shore of Lake Superior, 1953–79.

have been generally considered as coarse fish. Suckers were the second largest contributors to the barrier catches and, over the years, their numbers have only been exceeded by rainbow smelt (*Osmerus mordax*). Suckers are widespread and were captured in nearly all weirs on Lake Superior. The longnose sucker is predominant in Lake Superior, whereas the white sucker is more prevalent in Lakes Michigan and Huron.

LAKE SUPERIOR

The annual numbers of migrating rainbow trout captured in selected streams of Lake Superior were available after the installation of the sea lamprey barriers in 1953. The number of large (over 30 cm) rainbow trout handled at the eight index barriers on the south shore never exceeded 2000 fish per year (Fig. 2), and the highest number killed was 280 fish in 1973. The number of fish captured at a weir is not indicative of the total population utilizing the stream. Many rainbow trout migrate upstream in the fall and remain in the stream over winter to spawn in the spring (Neimuth 1970). Some rainbow trout migrate before the installation of the weirs in the spring, and still others are reluctant to enter the traps and may spawn below the barrier or migrate to other streams. Recent evidence of rainbow trout reaching the spawning beds before barrier activation in the spring was provided on the Brule River. Wisconsin State personnel, operating a fishway located above a sea lamprey index weir on the Brule River, captured some 2000 mature rainbow trout between October 1978 and March 1979 (P. Peters, Wisconsin Department of Natural Resources, Brule, Wisconsin, personal communication). The weir operation in the spring of 1979 passed 589 live rainbow trout and electrocuted 8.

The average numbers of large rainbow trout killed at the eight index weirs annually from 1953 to 1979 in the United States, and from 1956 to 1967 in Canada, were 127 and 115 fish, respectively. Mortality of spawning rainbow trout was insignificant when compared with the population of rainbow trout occurring in Lake Superior and its tributaries. A creel census conducted in 1952 estimated that nearly 75 000 rainbow trout were caught by anglers in the State of Michigan. Because of increased stocking rates by the State of Michigan, the rainbow trout population has increased so that between 300 000 and 500 000 rainbow trout (A. T. Wright, Michigan Department of Natural Resources, Lansing, Michigan, personal communication) are now harvested in the State of Michigan, with the majority of the fish being caught in the Great Lakes and their tributaries.

The number of suckers handled at the United States weirs (Fig. 3) during April–July was limited by the capacity of the traps. A mark and recapture study on the Brule River indicated ~350 000 suckers in the river below the weir; however, the trap, as fished, only caught 1000 fish per day. Similarly, 100 000 fish were estimated below the weir on the Huron River and only 800 fish per day were caught in the traps. Blocking of fish migration is common at all weirs, and the numbers of suckers handled was only a portion of the sucker population in the river. Moreover, suckers spawn along the lakeshore, further limiting the impact of the weirs on their population. The number of fish killed represents a small percentage of the fish subjected to the hazard of the weir. Thus, a comparison of the trap catch with the number killed does not represent a true percentage mortality for the species.

The average mortality at the eight Canadian barriers on Lake Superior was 3071 white and 1571 longnose suckers per year, whereas the average numbers from eight United States weirs were 1398 white and 2810

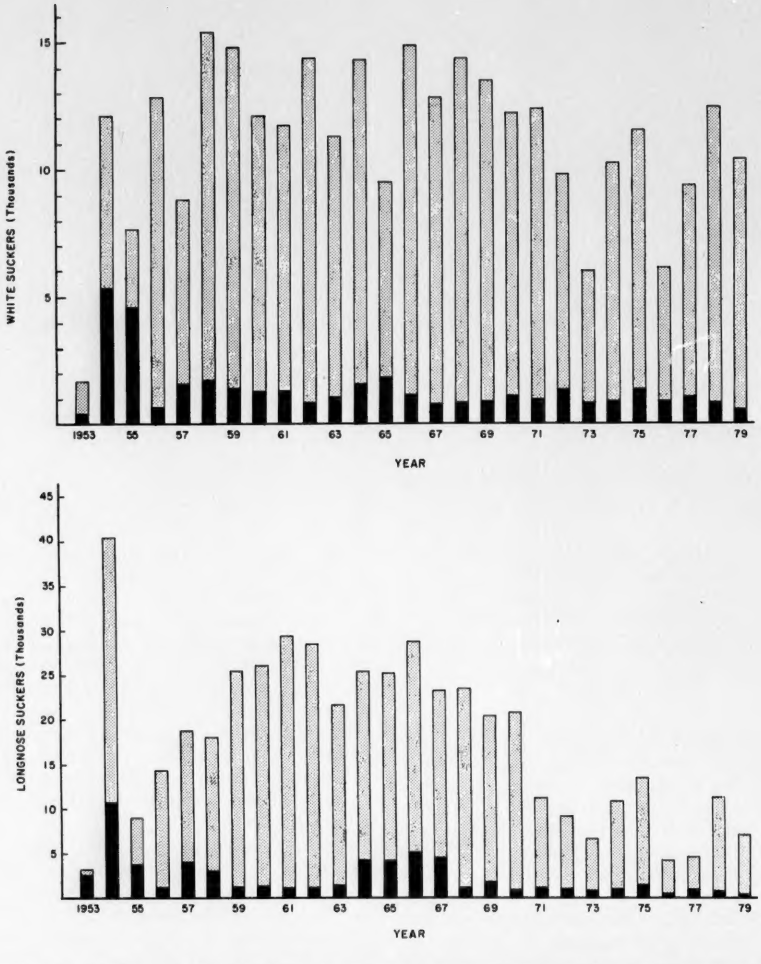

FIG. 3. Numbers of white suckers (*Catostomus commersoni*) (upper) and longnose suckers (*Catostomus catostomus*) (lower) handled (open bars) and number killed (solid bars) at eight weirs on the south shore of Lake Superior, 1953–79.

longnose suckers per year. The largest fish kill at a barrier on Lake Superior was on the Bad River, Wisconsin, in 1956, where 16 000 white and 4000 longnose suckers were killed.

The numbers of brook trout killed at all index barriers were estimated to be in the low thousands, and the majority of the fish were juveniles. Brook trout spawn in the fall and are not normally found near the barriers during the period of operation.

Some rainbow trout and suckers develop morphological damage while subjected to electric shock. Larger fish are vulnerable to injury because of the high voltage gradient required to stop sea lampreys at the barrier. Displaced vertebrae are quite common in suckers; Neimuth (1970) estimated that 6% of the large rainbow trout in the Brule River were disfigured because of damaged vertebrae. The injured vertebrae heal, as evidenced by the return of disfigured suckers to the weirs in successive years. Injuries caused by electric shock are rarely fatal to rainbow trout, but fishermen generally are displeased when they catch disfigured fish. The potential damage inflicted by the more subtle effects of electroshock is unknown but is considered inconsequential.

LAKE MICHIGAN

The operation of up to 49 weirs along the north shore of Lake Michigan from 1954 to 1960 resulted in a total mortality of 218 754 white and only 287 longnose suckers. The most notable kill amounted to 158 000 white suckers in the Pensaukee River in 1956. This incident was responsible for 86% of the white sucker mortality during the 7 years of weir operations on northern Lake Michigan streams. Only 352 (70 killed) rainbow trout were trapped at the Lake Michigan weirs in the 7-yr operating period.

LAKE HURON

Electrical barrier operation began in Canadian Lake Huron tributaries in 1965. The number of functional weirs during any given year varied from 4 to 10. The total fish mortality for the 14-yr period through 1978 was 151 000 white suckers, 8000 longnose suckers, and 900 large rainbow trout. Twelve thousand white suckers were killed at the Bayfield River weir in 1971, and 66% of the white sucker mortality on Lake Huron occurred on the Harris–Naiscoot and Bayfield rivers during the years of operation. Approximately 200 brown trout (*Salmo trutta*) were killed at the 12 barriers during the 14-yr period (over 50% were less than 30 cm long).

Lawrie (1954) noted that brown bullhead (*Ictalurus nebulosus*) was highly successful in avoiding electrocution at the electrical barriers. A study in the mid-1970s of barrier catch data from Lake Huron showed that the number of individuals electrocuted for one live-trapped specimen was:

Bowfin (*Amia calva*)	9.47 to 1
Small white sucker	1.19 to 1
Rainbow trout	0.17 to 1
Rock bass (*Ambloplites rupestris*)	0.13 to 1
Brown bullhead	0.05 to 1

Thus, whereas the bowfin is extremely vulnerable to electrocution by the control weirs, the brown bullhead is highly resistant.

Effects of Chemical Control on Fishes

TREATMENTS WITH TFM AND TFM-BAYER 73

In 1958 the stream-dwelling fishes of Lake Superior were subjected to an additional hazard from sea lamprey control operations — the addition of the lampricide TFM. Although the chemical is selectively toxic to lampreys, some fish are often killed. Fish in spawning condition are usually more vulnerable to the toxicant than at other times of the year; therefore, chemical treatments are generally scheduled to avoid major spawning runs. Of the 1300 stream treatments performed since 1958, unusually high fish mortalities occurred in about 40. With few exceptions, these fish kills have not been as large as some caused by operation of electrical barriers.

In the United States, the greatest number of large fish killed were suckers (both white and longnose), with decreasing numbers of northern pike (*Esox lucius*), brown trout, and walleye (*Stizostedion vitreum vitreum*). In Canada, suckers are by far the most heavily affected species; however, brown bullhead, rainbow trout, brook trout, coho salmon (*Oncorhynchus kisutch*), and northern pike have also suffered from the effects of TFM.

More notable lampricide-induced fish mortalities and numbers affected were as follows: Cedar River, Lake Michigan: 25 000 white and 5000 longnose suckers; Muskegon River, Lake Michigan: 12 500 northern pike, 10 000 white suckers, and 1000 walleyes; Brule River, Lake Superior: 14 500 white suckers; Nottawasaga River, Lake Huron: 10 000 white suckers, 5000 walleyes, and 5000 carp (*Cyprinus carpio*); Root and Spanish rivers, Lake Huron: 10 000 white suckers each; Little Salmon River, Lake Ontario: 10 000 brown bullheads; and the Little Manistee River, Lake Michigan, and Rifle River, Lake Huron: 2000 brown trout each. Other fish kills considered as major were in the magnitude of from 1000 to 5000 fish.

High mortality among small forage fish species, many of which are resident to the streams, occasionally occurred, and minor fish kills are encountered regularly, particularly below application sites of TFM. While these mortalities were not as well documented as those of the larger species, subsequent surveys and treatments suggested substantial recoveries for most species. Evidence is not available of any dramatic depletion of such species, other than the stonecat. Long-term effects of repeated treatments, where subtle trends might be experienced, cannot be addressed. The forage fish most often affected are common shiner (*Notropis cornutus*), johnny darter (*Etheostoma nigrum*), longnose dace (*Rhinichthys cataractae*), blacknose dace (*Rhinichthys atratulus*), spottail shiner (*Notropis hudsonius*), brook stickleback (*Culaea inconstans*), and sculpin (*Cottus* spp.).

Other species including trout-perch (*Percopsis omiscomaycus*), logperch (*Percina caprodes*), bullhead (*Ictalurus* spp.), and mudminnow (*Umbra limi*) are sometimes adversely affected by chemical treatments (Smith et al. 1974). The distribution of these species is much wider along the southern shore of Lake Superior than is the stonecat (Moore and Braem 1965); and the populations have not been reduced significantly since some of the streams are rarely treated, and recruitment from the lake is possible for the first two species.

The high degree of selection for mortality of one or a few species is often striking when a large fish kill occurs. Further, it is not unusual to observe spawning adults affected rather quickly by the chemical, whereas juveniles of the same species are not bothered. This has been most noticeable with dace and logperch but is apparently true of other species, including some of the Great Lakes salmonids.

TABLE 1. Numbers of stonecats (*Noturus flavus*) trapped and killed at electrical barriers, and years of lampricide treatments (indicated by asterisk) on two selected streams, 1958–79.

	Brule River		Amnicon River	
Year	No. trapped	No. killed	No. trapped	No. killed
1958	808	20	469*	77
1959	417*	9	59	6
1960	279	1	5	3
1961	160	0	1	2
1962	24*	3	8*	0
1963	7	0	0	1
1964	8	0	4	1
1965	8*	0	1	4
1966	0	0	18	5
1967	1	0	1*	3
1968	2	0	1	0
1969	0*	0	0	0
1970	1	0	0	1
1971	6	0	6*	0
1972	3*	0	0*	1
1973	7	0	0	0
1974	6*	2	1	1
1975	8	0	4*	3
1976	4	1	2	2
1977	16*	1	14	1
1978	41	0	59*	0
1979	23	0	9	0
Total	1829	37	662	111

The detrimental effects of chemical treatments on a susceptible fish species can be demonstrated by comparing the number of stonecats handled on the Amnicon and Brule River weirs on the south shore of Lake Superior before and after treatment (Table 1). After the first treatment of the Amnicon River in 1958, dead stonecats were found throughout the treated area, and it was thought that the entire population of this species was eliminated (G. A. Anderson, U.S. Fish and Wildlife Service, Marquette, Michigan, personal communication). The stonecats in the Brule River were similarly affected, but some untreated tributaries provided a haven for a percentage of the population. The distribution of stonecats is limited to nine streams at the extreme western end of Lake Superior (Moore and Braem 1965). Five of the nine streams are treated on a regular basis, and it was feared that the species would be eliminated from Lake Superior through repeated treatments. However, the weir catches demonstrate that although the population is severely depressed, it has not been eliminated.

On Lake Ontario, a similar situation was noted in Oakville and Lynde creeks where it was believed that nearly complete kills of stonecats occurred in sections of both streams during treatments in 1971 and 1978, respectively. Stonecats are found in relatively low abundance in the tributaries of the northwest corner of Lake Ontario (Johnson 1965). With the high mortalities encountered, it is expected that their recovery will be slow.

The brown bullhead is equally as susceptible to TFM as the stonecat; however, its wide distribution and abundance ensures its survival. The brown bullhead reaches the upper limit of its range in the Great Lakes along the north shore of Lake Superior, and it may be seriously affected in this area from lampricide treatments.

Resident brook trout do not appear to suffer significant mortality at the weirs or from chemical treatments. These fish are found in relatively large numbers in five of the eight streams in the Lake Superior evaluation network. Weirs on these streams are located near the estuaries where brook trout are normally not abundant. An average of 489 brook trout were captured annually with a mortality rate less than 8% (Table 2). The five streams were treated 45 times with lampricide since 1958, and two of these, the Silver and Sucker rivers, were treated 12 and 14 times, respectively. Although barrier catches varied from year to year, the records indicate little damage to brook trout populations because of multiple streams treatments with TFM or by operation of the electrical barriers.

STREAM SURVEYS

The use of electric shockers to collect ammocoetes for survey purposes is another potential hazard to resident stream fish. It is considered that stream surveys with electrical shockers has had a minimal effect on fish populations. Since the sea lamprey ammocoete is sedentary, the surveyor makes no effort to conceal his presence, and by wading the stream elicits natural fright response from fishes. The silt–sand–clay habitat generally associated with lamprey larvae is only marginally used by most fish species, thereby precluding many contacts. Also, substrate of this type is normally more conductive than the overlying water, and much of the electric current enters the stream bed and is not available to affect fish. The slow, methodical coverage of the ammocoete habitat leaves ample time for the "fright and flight" response of fishes as they escape the electrical field. Subtle, reversible changes in body chemistry and behavior are possible, which would make the affected fish temporarily more vulnerable to predation (Patten and Gillaspie 1966; Vibert 1967; Madden and Houston 1976; Schreck et al. 1976).

GRANULAR BAYER 73 FOR SURVEYS AND TREATMENTS

Another survey technique involves a granular formulation of Bayer 73 used as a bottom toxicant (Great Lakes Fishery Commission 1967). This heavy formulation sinks and releases the toxicant near the bottom of the stream or bay area. Fishes which are physiologically bound to the bottom, such as darters and sculpins, are most vulnerable to this type of survey; however, since the toxicant remains near the bottom,

TABLE 2. Annual numbers of brook trout (*Salvelinus fontinalis*) trapped and killed at electrical barriers, and years of lampricide treatment (indicated by asterisk), on five selected rivers on Lake Superior, 1953–79.

	Two Hearted		Sucker		Chocolay		Silver		Brule	
Year	Trap	Kill	Trap	Kill	Trap	Kill	Trap	Kill	Trap	Kill
1953	24	2	23	2	—	—	—	—	—	—
1954	13	2	80	10	57	7	10	45	—	—
1955	26	8	110	6	96	74	20	37	—	—
1956	45	2	52	7	59	3	96	2	—	—
1957	24	1	16	1	72	14	64	1	19	0
1958	37	1	596*	14	88*	12	104*	10	9	0
1959	34*	1	390*	26	110	20	146	10	16*	0
1960	36	1	321	9	64	17	129	6	108	0
1961	128	12	304*	12	65*	10	87*	8	24	0
1962	40*	5	394	3	79	8	14	11	4*	0
1963	72	5	489*	7	99	6	65	16	14	0
1964	59	14	226	1	56	28	73	6	10	0
1965	31*	11	113*	15	55	34	18	3	4*	0
1966	31	11	64	5	63*	12	10*	3	2	0
1967	21	7	62*	6	15	1	30	1	10	0
1968	51	1	631	11	63	5	48	4	9	0
1969	24	4	489*	10	168	9	47*	1	123*	0
1970	46*	8	304	16	138*	32	59	10	10	0
1971	18	6	235*	16	55	11	44	7	164	0
1972	13	6	183*	25	36	12	16*	4	13*	0
1973	36*	9	330*	33	81*	9	27*	8	19	0
1974	43	4	436*	16	74	9	27*	3	29*	0
1975	45*	0	294*	10	123	5	55*	8	52	0
1976	13	4	231	9	205	7	6*	14	15	0
1977	27	13	263*	0	86	0	32*	6	7*	0
1978	20	0	64	3	175	15	30*	0	36	0
1979	16*	2	78*	5	241	39	20*	0	21	0
Total	973	140	6778	278	2423	399	1277	224	718	0

minimum swimming effort is required to avoid the toxic zone.

A problem arises when large areas of estuarine habitat are covered with granules, and the fish cannot escape the effects of the chemical. During treatment of the estuary of the Sand River on the north shore of Lake Superior in 1969, 800 white and longnose suckers died. A similar occurrence in the estuary of Gawas (Sucker) Creek, Lake Huron, in 1978, involved hundreds of fish, including suckers, northern pike, yellow perch (*Perca flavescens*), bullheads, and various minnow species.

Fish kills of this magnitude are rare from the use of granular Bayer 73 and relatively little fish mortality has been experienced. However, the July 1979 granular Bayer treatments, conducted on three lentic water areas along Lake Superior's north shore, dramatically emphasized a situation of concern when using this toxicant. These applications, carried out about 1 mo earlier than usual, in cool water temperatures, resulted in large fish kills unexpected from past experience at these sites. It was estimated that over 2000 juvenile whitefish (tentatively identified as round whitefish, *Prosopium cylindraceum*) and some 500 sticklebacks were killed, as well as a number of longnose suckers and other species.

Discussion

The restoration and maintenance of salmonids in the Great Lakes are predicated on sea lamprey control. The damage to resident and migratory fish populations in streams as a result of sea lamprey control has been minimal considering the magnitude of the program. Suckers have suffered the greatest losses, with no apparent effect on the total population. Recent estimates are that 1588 t (1 t = 1000 kg) of suckers per year could be harvested from the upper three Great Lakes without damaging the stocks (Gould 1979). The number of rainbow trout has been on the rise as a result of increased fish stocking and decreased sea lamprey predation, as dramatically shown by weir catch records and sports fishing statistics (Ellefson and Jamson 1971).

Of the control methods used, the electric weirs had the most damaging effect on large migratory fish. The 3- to 4-mo operating period which coincided with the spawning runs of rainbow trout and suckers was responsible for much of the mortality. In addition, the weirs blocked some fish from their preferred spawning habitat. The electric barrier network, for sea lamprey assessment purposes, was terminated in 1979.

Chemical treatments were responsible for some major fish kills, particularly in earlier TFM–Bayer 73 combination treatments. In later years, chemical treatments were scheduled to avoid many of the major concentrations of migratory fish. The interval between treatments and the short time of chemical exposure minimizes the possibility of repeated fish kills. A continued and persistent problem is the mortality of a small number of resident species in most treatments. These mortalities appear insignificant unless a highly susceptible fish, such as the stonecat, is encountered. Long-term effects on stream fish populations from intensive treatment with lampricide are as yet unknown. Until integrated control is able to reduce further the frequency of chemical treatments, or an alternate solution is found to the sea lamprey problem, fish kills will continue as a "necessary evil."

A statement by Erkkila et al. (1956) still has application: "If the conditions of sea lamprey control cause some fish kill, the mortality should be considered part of the cost of operations." One of the major goals of the sea lamprey control program is to minimize this cost.

APPLEGATE, V. C., J. H. HOWELL, A. E. HALL JR., AND M. A. SMITH. 1957. Toxicity of 4,346 chemicals to larval lampreys and fishes. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 207: 157 p.

APPLEGATE, V. C., J. H. HOWELL, J. W. MOFFETT, B. G. H. JOHNSON, AND M. A. SMITH. 1961. Use of 3-trifluormethyl-4-nitrophenol as a selective sea lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 1: 35 p.

APPLEGATE, V. C., AND B. R. SMITH. 1950. Sea lamprey spawning runs in the Great Lakes, 1950. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 61: 49 p.

APPLEGATE, V. C., B. R. SMITH, A. L. MCLAIN, AND M. PATTERSON. 1952a. Sea lamprey spawning runs in the Great Lakes, 1951. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 68: 37 p.

APPLEGATE, V. C., B. R. SMITH, AND W. L. NIELSEN. 1952b. Use of electricity in the control of sea lampreys: electromechanical weirs and traps and electrical barriers. U.S. Fish Wildl. Serv. Sci. Rep. Fish. 92: 52 p.

BALDWIN, N. S., AND R. W. SAALFELD. 1962. Commercial fish production in the Great Lakes 1867–1960. Great Lakes Fish. Comm. Tech. Rep. 3: 166 p.

ELLEFSON, P. V., AND G. C. JAMSON. 1971. Michigan's salmon–steelhead trout fishery: an economic evaluation. Pap. Mich. Acad. Sci. Arts Lett. 4: 237–244.

ERKKILA, L. F., B. R. SMITH, AND A. L. MCLAIN. 1956. Sea lamprey control on the Great Lakes, 1953 and 1954. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 175: 27 p.

GOULD, W. 1979. A new image for an old sucker. *In* The Fisherman. Vol. 31(2). The Marine Publishing Co., Grand Haven, MI.

GREAT LAKES FISHERY COMMISSION. 1967. Annual report for the year 1966. Great Lakes Fish. Comm., Ann Arbor, MI. 61 p.

HOWELL, J. H., E. L. KING JR., A. J. SMITH, AND L. H. HANSON. 1964. Synergism of 5,2′-dichloro-4′-nitrosalicylanilide and 3-trifluoromethyl-4-nitrophenol in a selective lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 8: 21 p.

JOHNSON, M. G. 1965. Estimates of fish populations in warmwater streams by the removal method. Trans. Am. Fish. Soc. 94: 350–357.

LAWRIE, A. H. 1954. Report on the operation of electrical barriers in the Sault Ste. Marie district. Annu. Rep. to Great Lakes Research Committee, 1954, by J. M. Speirs, Secretary. Section 2, App. 8: 15 p.

LENSON, W. J., AND A. H. LAWRIE. 1959. The engineering aspects of sea lamprey barrier design and operation. Fish. Res. Board Can. Prog. Rep. Biol. Sta. Tech. Unit (London, Ont.) 1: 9–14.

MADDEN, J. A., AND A. H. HOUSTON. 1976. Use of electroanaesthesia with freshwater teleosts: some physiological consequences in the rainbow trout, *Salmo gairdneri* Richardson. J. Fish. Biol. 9: 457–462.

MCCAULEY, R. W., AND A. B. LOUCKS. 1959. The experimental barrier on the Bridgeland River. Annu. Rep. Fish. Res. Board Can. Biol. Sta. (London, Ont.) Apr. 1, 1959–Mar. 31, 1960. Append. 49: 94.

MCLAIN, A. L. 1957. The control of the upstream movement of fish with pulsated direct-current. Trans. Am. Fish. Soc. 86(1956): 269–284.

MCLAIN, A. L., AND W. L. NIELSEN. 1953. Directing the movement of fish with electricity. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 93: 24 p.

MCLAIN, A. L., B. R. SMITH, AND H. H. MOORE. 1965. Experimental control of sea lampreys with electricity on the south shore of Lake Superior, 1953–60. Great Lakes Fish. Comm. Tech. Rep. 10: 48 p.

MOORE, H. H., AND R. A. BRAEM. 1965. Distribution of fishes in U.S. streams tributary to Lake Superior. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 516: 61 p.

NEIMUTH, W. 1970. A study of migratory lake run trout in the Brule River, Wisconsin, Part II, rainbow trout. Bureau of Fish Management Rep. 38. Wis. Dep. Natural Resources. 69 p.

PATTEN, B. G., AND C. C. GILLASPIE. 1966. The Bureau of Commercial Fisheries type IV electrofishing shocker — its characteristics and operation. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 529: 15 p.

SCHRECK, C. B., R. A. WHALEY, M. L. BASS, O. E. MAUGHAN, AND M. SOLAZZI. 1976. Physiological responses of rainbow trout (*Salmo gairdneri*) to electroshock. J. Fish. Res. Board Can. 33: 76–84.

SMITH, B. R. 1971. Sea lampreys in the Great Lakes of North America, p. 207–247. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London.

SMITH, B. R., J. J. TIBBLES, AND B. G. H. JOHNSON. 1974. Control of the sea lamprey (*Petromyzon marinus*) in Lake Superior, 1953–70. Great Lakes Fish. Comm. Tech. Rep. 26: 60 p.

VIBERT, R. 1967. General report of the working party on the application of electricity to inland fishery biology and management, p. 3–51. *In* R. Vibert [ed.] Fishing with electricity — its applications to biology and management. F. A. O., U. N., Fishing News (Books) Ltd., London.

Effects of Sea Lamprey (*Petromyzon marinus*) Control in the Great Lakes on Aquatic Plants, Invertebrates, and Amphibians[1]

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GILDERHUS, P. A., AND B. G. H. JOHNSON. 1980. Effects of sea lamprey (*Petromyzon marinus*) control in the Great Lakes on aquatic plants, invertebrates, and amphibians. Can. J. Fish. Aquat. Sci. 37: 1895–1905.

The chemicals 3-trifluoromethyl-4-nitrophenol (TFM) or a combination of TFM and 2′,5-dichloro-4′-nitrosalicylanilide (Bayer 73) have been used to control the sea lamprey (*Petromyzon marinus*) in the Great Lakes for about 20 yr. These chemicals cause some mortalities of Oligochaeta and Hirudinea, immature forms of Ephemeroptera (*Hexagenia* sp.), and certain Trichoptera, Simuliidae, and Amphibia (*Necturus* sp.). The combination of TFM and Bayer 73 may affect some Pelecypoda and Gastropoda, but its overall effects on invertebrates are probably less than those of TFM alone. Granular Bayer 73 is likely to induce mortalities among oligochaetes, microcrustaceans, chironomids, and pelecypods. No evidence exists that the lampricides have caused the catastrophic decline or disappearance of any species. The overall impact of chemical control of sea lampreys on aquatic communities has been minor compared with the benefits derived.

Key words: sea lamprey control, Great Lakes, TFM, Bayer 73, aquatic plants, invertebrates, amphibians

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Les substances chimiques 3-trifluorométhyl-4-nitrophénol (TFM) ou une combinaison de TFM et de 2′,5-dichloro-4′-nitrosalicylanilide (Bayer 73) ont été utilisées dans le contrôle de la grande lamproie marine (*Petromyzon marinus*) dans les Grands Lacs pendant environ 20 ans. Ces substances causent une certaine mortalité chez les Oligochaeta et Hirudinea, les formes immatures d'Ephemeroptera (*Hexagenia* sp.) et certains Trichoptera, Simuliidae et Amphibia (*Necturus* sp.). La combinaison TFM et Bayer 73 peut affecter certains Pelecypoda et Gastropoda mais, dans l'ensemble, ses effets sur les invertébrés sont probablement moindres que ceux de TFM seul. Bayer 73 granuleux est susceptible de déclencher des mortalités parmi les oligochètes, microcrustacés, chironomides et pélécypodes. Nous n'avons pas de preuve que les lampricides ont causé le déclin ou la disparition catastrophiques d'aucune espèce. L'éffet global du contrôle chimique de la grande lamproie marine sur les communautés aquatiques a été minime comparativement aux avantages qui en ont découlé.

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SEA lamprey control in tributaries of the Great Lakes began with installation of mechanical and electrical barriers (weirs) in the 1950s to block adult lampreys from their spawning grounds. The control of sea lampreys with chemicals began in 1958 with the application of 3-trifluoromethyl-4-nitrophenol (TFM) to tributary streams to kill the larval lampreys burrowed in the stream bottom. In 1963, it was discovered that the addition of small amounts of 2′,5-dichloro-4-′nitrosalicylanilide (Bayer 73) (up to 2%) significantly reduced the amount of TFM needed in stream treatments and similarly reduced the cost of treatment (Howell et al. 1964). Combinations of TFM and Bayer 73 have been used since 1963 for treatment of the larger tributaries of the Great Lakes. Most of the more than 400 tributaries found to harbor sea lampreys have been treated with either TFM or the mixture, and many have been treated several times in the 21-yr time span.

Early efforts at lamprey control were concentrated on the stream environments, but in the early 1960s, significant populations of ammocoetes were found to in-

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habit certain lentic areas in inland lakes and the Great Lakes near the mouths of lamprey-spawning streams. The lentic areas were difficult to survey, and collection efforts with bottom dredges or electric trawls did not reveal the full extent of these lentic populations. In 1966, a granular formulation of Bayer 73 (5% active ingredient) was shown to be an irritant that caused larval lampreys to leave their burrows and swim to the surface of the water where they could be collected (E. L. King Jr., and J. H. Howell, U.S. Bureau of Sport Fisheries and Wildlife, Great Lakes Fishery Laboratory, Administrative Report, 1970, mimeograph). This chemical technique provided better estimates of ammocoete populations and made it possible to survey lentic habitats effectively. Bayer 73 also acts as a lampricide and since 1966, many lentic areas in the Great Lakes drainage have been treated with the chemical.

Although the primary studies on lampricide chemicals were directed toward the development of efficient and effective methods to control lampreys, some studies have been made on the effects of the chemicals on other aquatic organisms.

The objective of this paper is to review the existing information on the effects of lampricides on plants, invertebrates, and amphibians in aquatic habitat and to provide an assessment of the observed and potential impact of lampricides on populations of these organisms.

TFM

STREAM TREATMENTS

The lampricide is applied at one or more points in a stream, depending on the extent of the stream system, the velocity and flow patterns, and the concentrations needed for effective control of lampreys in the particular stream. The amount of chemical applied at each point is that which will maintain a concentration lethal to lampreys to the next application point downstream, without exceeding the maximum concentration that is safe for salmonid fishes. Therefore the areas of the stream just downstream from application points are often exposed to much higher concentrations of the chemical than are some other areas farther downstream. The minimum effective and maximum allowable concentrations are usually 1–3 and 3–9 mg/L, respectively, in Lake Superior tributaries, and 2–8 and 6–16 mg/L, respectively, in tributaries to Lakes Michigan and Huron (Smith and Braem 1976).

FACTORS AFFECTING TOXICITY

The minimum effective concentration of TFM for control of sea lampreys varies considerably from stream to stream. In tributaries to Lake Huron treated in 1975, the minimum effective concentration ranged from 1.5 mg/L in the Carp River to 11.0 mg/L in the Pine River.

Dawson et al. (1975) demonstrated that temperature has little influence on the toxicity of TFM and that the toxicity of the compound to larval sea lampreys decreases as pH and hardness of the water increase. Marking and Olson (1975) demonstrated that pH and hardness also affected the toxicity of TFM to bony fishes, but found that the toxicity of the chemical generally increased as water temperatures increased.

It has not been conclusively determined that the toxicity of TFM to plants and invertebrates is affected to the same degree by the same factors that affect the toxicity to sea lamprey larvae and other fish. Kawatski et al. (1975) showed that the toxicity of TFM to *Chironomus tentans* was decreased by high pH and hardness. Fremling (1975) showed a similar trend for *Hexagenia* mayflies and demonstrated a 60-fold decrease in toxicity between pH 6.5 and 9.5. Therefore, it appears that the relative toxicity of TFM to invertebrates follows approximately the same pattern from stream to stream as does the toxicity to lampreys, and that the safety index between invertebrates and lampreys is relatively constant. Concentrations of TFM in this paper are expressed as active ingredient, and the terms such as sensitive, resistant, and highly resistant are used to provide only general comparisons of the sensitivity of nontarget organisms with that of larval sea lampreys.

TYPES OF STUDIES

Numerous investigators have observed the effects of TFM on invertebrates in laboratory tests or in the field before and after stream treatments. Comparisons of results between investigators are difficult because laboratory tests were done in waters with widely different chemical characteristics, and few of the investigators included sea lamprey larvae in their tests. Thus it is difficult to establish the relative sensitivity of lampreys to that of other organisms in a particular type of water. Furthermore, field studies generally have not included enough replicate samples to lend statistical validity to the results. However, an examination of the overall data contributed by the several laboratory and field studies establishes trends and provides sufficient information on which to base certain conclusions.

The sources of data cited here as listed as (1) laboratory studies (also referred to as 24-h tests or LC50 values), (2) field studies, and (3) treatment summaries. The more comprehensive laboratory studies were done by Smith (1967) and Maki et al. (1975a), in which large numbers of organisms were exposed to TFM under relatively controlled conditions. In field studies, Torblaa (1968) sampled seven treated streams and two untreated streams, some for up to 6 wk after treatment and others up to 1 yr. Haas (1970) sampled before and 3–4 d after two separate treatments in a single stream. Treatment summaries consisted of notes and nonprecise estimates of mortality gleaned from summary sheets of past stream treatments done by the Ludington and Marquette Biological Stations in Michigan. The observations were summarized by lake basin and by organism. If a treatment report did not contain observations on mortality of nontarget organisms, there was no way to determine whether there was any mortality, or whether any observations were made. Therefore, the percentage occurrence of mortality of any particular organism given represents the percentage of the total number of times mortality of any organism was recorded, not the percentage of times mortality occurred out of the total number of treatments done. For example, in Lake Superior tributaries, 37 treatment reports contained observations of mortality, and 17 of those, or 46%, included mayflies.

EFFECTS ON PLANTS

Maki et al. (1975b), who conducted laboratory tests on the effects of TFM on 10 species of algae in pure cultures, found that most species tested experienced a 50% inhibition of growth at less than 10 mg/L of active ingredient. Blue-green algae were generally most resistant (9–10 mg/L), green algae were intermediate (4–5 mg/L), and diatoms the most sensitive (1–3 mg/L). Concentrations of 30 mg/L did not destroy the viability of the cells, but temporarily inhibited growth. Tests in artificial streams showed that TFM inhibited community metabolism, reflecting in part, the effects on algal growth (Maki and Johnson 1976).

Although TFM does affect algal growth, and may temporarily inhibit stream productivity, rapid flushing of the chemical from the stream after treatment and the redistribution of unaffected algae from above the treatment site should limit adverse effects to short periods of time.

The effects of TFM on aquatic macrophytes can be severe at high concentrations, but appear to be low at concentrations used for sea lamprey control. Josephs (1961), who originally patented various salts of TFM as aquatic herbicides, presented evidence that TFM controlled common aquatic plants such as *Anacharis*, *Cabomba*, and *Ceratophyllum* at concentrations of 15–25 mg/L in standing water and 100 mg/L in flowing water.

In laboratory tests, Maki and Johnson (1977) showed TFM to inhibit growth of *Elodea canadensis* and *Myriophyllum spicatum* at concentrations of 10 mg/L and above in exposures of 1 h or more. The authors estimated that a treatment necessary to eliminate lampreys in the water they used could cause a 5–10% reduction in growth in *Elodea* and a 20% reduction in *Myriophyllum*.

Macrophytes are not abundant in lamprey-producing streams because such streams are generally fast flowing and have predominantly coarse bottom materials. Therefore, effects of TFM on aquatic plants will likely have little impact on productivity of the stream ecosystem.

EFFECTS ON INVERTEBRATES

Aquatic worms — Aquatic worms appear to be very sensitive to TFM. Smith (1967) showed 100% mortality of turbellarians at 8 mg/L in 24-h exposures, when sea lampreys were eliminated by 4 mg/L. Oligochaetes had 24-h LC50 values of 3.4–6.6 mg/L (Chandler and Marking 1975; Maki et al. 1975a; Table 1).

TABLE 1. Toxicity of field grade TFM (active ingredient) to selected macroinvertebrates in laboratory tests (data adapted from Maki et al. 1975a). Unless specified, insect nymphs and larvae were late instars.

Organism	Size (mm)	24-h LC50 (mg/L)	95% confidence interval (mg/L)
Pelecypoda			
Pisidium sp.	10–12	16.9	14.93–19.13
Sphaerium sp.	10–15	17.5	16.84–18.21
Ligumia sp.	<9	>11.2	—
Ligumia sp.	>16	>18.0	—
Isopoda			
Asellus militaris	8–10	17.0	14.41–20.06
Amphipoda			
Gammarus pseudolimnaeus	10–12	38.0	32.76–44.08
Decapoda			
Orconectes propinquus	30–40	>36.4	—
Ephemeroptera			
Baetis sp.		6.9	6.39–7.45
Hexagenia bilineata		7.9	6.93–9.01
Cloeon sp.		11.1	8.88–13.87
Isonychia bicolor		18.3	15.77–21.23
Stenonema frontale		24.9	22.23–27.89
Tricorythodes sp.		29.3	25.86–33.19
Stenonema luteum		29.6	27.92–31.37
Paraleptophlebia		>34.6	—
Baetisca obesa		37.8	33.16–43.09
Ephemerella cornuta	<4	36.2	31.75–41.27
E. cornuta	8	>39.0	—
Odonata			
Ophiogomphus sp.		>38.0	—
Plecoptera			
Isoperla slossonae		16.7	13.47–20.71
Paragnetina media		21.5	17.92–25.81
Pteronarcys dorsata		32.2	23.85–43.47
Acroneuria lycorias		>34.0	—
Megaloptera			
Cauliodes sp.		>36.0	—
Trichoptera			
Chimarra obscura		3.8	3.59–4.04
Brachycentrus americanus		10.5	8.40–13.13
Lepidostoma sp.		15.0	13.64–16.50
Cheumatopsyche sp.		28.3	24.71–32.40
Hydropsyche sp.		>32.0	—
Macronemum sp.		>38.0	—
Limnephilus consocius		>39.0	—
Diptera			
Simulium pugetense		6.1	5.65–6.59
Annelida			
Lumbricidae	60–90	6.6	6.11–7.13

Maki et al. (1975a) stated that aquatic earthworms could be reduced by 50% or more by stream treatments. Treatment summaries showed some mortality of earthworms in 40% of the observations in Lake Superior tributaries and 23% in Lake Michigan tributaries, and some of those were interpreted as massive mortalities.

Crustaceans — Crustaceans appear to be very resistant to TFM (Table 1). Chandler and Marking (1975) determined the 24-h LC50 for TFM against *Daphnia magna* to be 26 mg/L. Smith (1967) observed only 2.7% mortality of isopods (*Asellus*) at 20 mg/L of TFM, and Maki et al. (1975a) recorded a 24-h LC50 of 17 mg/L for the same organism. Amphipods (*Gammarus* sp.) were found to be even more resistant by Maki et al. (1975a) and Sanders and Walsh (1975) who reported comparable 24-h LC50s of 38 and 36 mg/L, respectively. Smith (1967) observed only 10% mortality of these organisms in 24-h tests at 20 mg/L. In the field, Torblaa (1968) reported a decline in numbers of amphipods in two streams, and Maki (1974) noted a sharp rise in drift rates of amphipods in artificial streams tested with TFM. The declines observed by Torblaa (1968) may have been due to drift of amphipods out of the sampling areas, and not to actual mortality.

Crayfish apparently are the most resistant of the crustaceans; 24-h LC50s of 36–46 mg/L were reported by Maki et al. (1975a) and Sanders and Walsh (1975). No mortality of crayfish was noted in field studies, but light mortalities were recorded in 5% of the observations in treatment summaries from Lake Michigan tributaries and 13% of those from Lake Superior tributaries.

Laboratory and field data indicate that it is unlikely that significant mortality of crustaceans would be caused by concentrations of TFM used in stream treatments for sea lamprey control.

Aquatic insects — Larvae and nymphs of aquatic insects vary greatly in their sensitivities to TFM, ranging from very sensitive to highly resistant, even within a single order. Generally, among insects as among invertebrates as a whole, organisms with well-developed exoskeletons are the most resistant to TFM.

Three of the insect orders appear to be particularly resistant to TFM. Maki et al. (1975a) or Smith (1967) gave 24-h LC50s of 36 mg/L for Megaloptera, 38 mg/L for Odonata, and 20 mg/L for Hemiptera. Field studies also indicated no adverse effects on these organisms. However, mortality was noted for Odonata in up to 20% and Hemiptera in up to 10% of the observations recorded in treatment summaries.

Stoneflies (Plecoptera), as a group, are among the more resistant insects in laboratory tests (Table 1). Smith (1967) killed only 30% of those organisms at 12 mg/L and 76% at 20 mg/L. Torblaa (1968) found a substantial decline in Nemouridae which persisted for several weeks in one stream, and Haas (1970) recorded a decline in *Taeneopteryx* in his study stream. Slight mortalities of stoneflies were noted in 13% (Lake Superior) to 19% (Lake Michigan) of the observations in treatment summaries. Overall, field data indicate only slight effects of TFM on stoneflies.

Mayflies (*Ephemeroptera*) have a wide range of resistance to TFM; some species are very susceptible and others highly resistant (Table 1). Maki et al. (1975a) stated that within a species, small sizes and early instars of mayflies are the most sensitive to TFM. Fremling (1975) found TFM to be most toxic to mayflies in water with a low pH and low total hardness.

Laboratory studies showed *Stenonema*, *Baetisca*, *Paraleptophlebia*, *Trichorythodes*, *Ephemerella*, *Callibaetis*, and *Isonychia* to be comparatively resistant to TFM, with 24-h LC50s ranging from 18 to 40 mg/L (Maki et al. 1975a; Chandler and Marking 1975). Smith (1967) reported similar findings for some of the same species. The mayflies found to be most sensitive in laboratory tests by Maki et al. (1975a) included *Cloeon*, *Baetis*, and *Hexagenia*. Smith (1967) showed 50% mortality of *Hexagenia* at 5 mg/L, and Fremling (1975) recorded 24-h LC50s for that genus ranging from 2.5 to 18.8 mg/L, depending on water hardness and pH. At pH 7.5 and lower, and at all water hardness tested, the 24-h LC50 was 7 mg/L or less. On the basis of their laboratory data, Maki et al. (1975a) and Fremling (1975) stated that concentrations of TFM used to control lampreys were likely to cause significant kills of mayflies.

Field studies by Torblaa (1968) and Haas (1970) each showed a trend toward reduced populations of mayflies, but none of the reductions appeared to be drastic. Torblaa (1968) recorded more sites at which there was no effect than sites at which a reduction was evident.

Mayflies (especially *Hexagenia*) were noted more often than any other organism among observations in treatment summaries. From 46 to 50% of the observations on invertebrates included dead mayflies, and in 17% of those in Lake Superior and 33% in Lake Michigan the numbers killed were large. Records of Canadian stream treatments also included occasional references to mortalities of mayflies. Several persons have reported what they interpreted to be premature emergence of mayflies during stream treatments (Applegate et al. 1961; R. Braem, Marquette Biological Station, Marquette, Michigan, personal communication). Maki et al. (1975a) documented this phenomenon in laboratory tests in which insect larvae exposed to TFM during late instar stages emerged as adults sooner than did the controls.

Caddis fly larvae (Trichoptera) also are variable in their sensitivity to TFM. Smith (1967), who differentiated between case building and net building caddis flies in his tests, noted an 8% mortality at 20 mg/L of TFM for 24 h for case builders and 44% for net builders. Maki et al. (1975a) demonstrated a 10-fold difference between their most sensitive and most resistant caddis fly larvae.

Torblaa (1968) recorded considerable declines (up to 94%) in numbers of caddis fly larvae in three of his study streams within 1 wk after treatment with TFM. Several other streams showed little or no change. Haas (1970) found declines in numbers of certain caddis flies in the Chocolay River after treatment.

The field treatment summaries indicate mortality of caddis flies in 30–33% of the observations, and about 10% of those involved large numbers. Thus, it appears that some species of caddis fly larvae are sensitive to TFM and subject to mortalities during stream treatments.

Coleoptera larvae were not included in any of the laboratory studies on toxicity of TFM. Torblaa (1968) found declines in Elmidae in three streams and an increase in one stream after treatment. The treatment summaries included beetle mortalities 5 and 17% of the time in Lake Superior and Lake Michigan tributaries, respectively. Beetles are not often a major component of the stream community or food chain, but they appear to be affected occasionally by stream treatments with TFM.

The Diptera appear to be resistant to TFM with the exception of black flies (Simuliidae). Both Smith (1967) and Maki et al. (1975a) found the 24-h LC50 for TFM to black flies to be 5–6 mg/L. Field samples taken by Torblaa (1968) included such small numbers of black flies that no conclusions could be drawn. None of the treatment summaries included observations on black flies, probably because the larvae are small, dark-colored, and soft-bodied, and therefore easily overlooked.

Snipe fly larvae (Rhagionidae) were found to be resistant by Smith (1967), who reported no mortality among larvae held in 20 mg/L of TFM for 24 h. Field studies by Torblaa (1968) and Haas (1970) showed no significant effects on this group.

Chironomids also are resistant to TFM; Smith (1967) reported a 24-h LC50 of more than 20 mg/L. Kawatski et al. (1975), who tested *Chironomus* in the laboratory, found the larvae to be immobilized by concentrations of 1–10 mg/L of TFM. However, most individuals recovered when placed in freshwater. Torblaa (1968) and Haas (1970) found rather drastic reductions in numbers of chironomids in some treated streams, but noted similar concurrent decreases in control streams, suggesting natural emergence as the cause.

Numbers of Tipulidae and Heleidae were reduced in some treated streams, but not in others (Torblaa 1968). Dead tipulids were noted in up to 30% of the observations in treatment summaries, but the numbers were always small. Laboratory data on these groups are not available.

Although certain species are sensitive to TFM, mortality of dipterans does not appear to be a widespread or serious side effect of TFM treatments.

Molluscs — Molluscs exhibited intermediate resistance to TFM in laboratory tests. The 24-h LC50 values for snails (*Physa*) were more than 20 mg/L (Smith 1967). Unionid clams were slightly less resistant with LC50s of 10 mg/L (Smith 1967) to 17.5 mg/L (Maki et al. 1975a). Molluscs were rare in the field studies by Torblaa (1968), and no strong trend was observed. In the stream treatment summaries, dead snails were noted in up to 11% of the observations and clams in up to 21%.

There were occasional reports of distressed clams with gaping valves during treatments with TFM in Canadian streams, but most recovered after the bolt of chemical passed. It appears that although molluscs are sometimes killed by stream treatments with TFM, populations are not decimated.

EFFECTS ON VERTEBRATES

Amphibians are the only vertebrates besides fish which have been observed to be affected by lampricides. No laboratory or field study data are known to be available on these organisms. However, field treatment summaries often referred to amphibians. Mortality of frog tadpoles was noted in 16% of the observations, and one observation referred to large numbers of dead tadpoles. Mud puppies (mostly *Necturus*) were noted in 32% of the observations in tributaries of Lake Superior and 36% in Lake Michigan, and up to 18% of those referenced large numbers killed. Mortalities of these amphibians are evidently common during stream treatments with TFM.

OVERALL EFFECTS OF TFM TREATMENTS

Available data on TFM from both laboratory tests and stream treatments indicate that some organisms are likely to be killed during any particular stream treatment. Those most likely to be affected include turbellarians, oligochaetes, leeches, mayflies (especially *Hexagenia*), some species of caddis flies, black flies, and mud puppies. Others which may be affected are beetle larvae (especially Elmidae), crane fly larvae, stoneflies, and clams. Kills of aquatic annelids and mayflies may involve substantial numbers during some treatments. Maki et al. (1975a) estimated that under conditions of their tests, aquatic earthworms, black fly larvae, and certain mayfly and caddis fly larvae could be reduced by 50% or more. Some studies indicate a temporary decrease in gross primary production (Maki and Johnson 1976) and significant reductions in density (numbers) of organisms (Maki 1974; Maki et al. 1975c). Maki (1974), however, found that TFM did not affect the diversity of organisms in artificial stream communities. Several groups appearing to be highly resistant in laboratory toxicity tests but showing some mortality in field observations were probably killed by high concentrations of TFM immediately downstream from application sites.

The effects of TFM on the nontarget portion of the stream community do not appear to be long lasting. Maki and Johnson (1976) found that community metabolism returned to normal within 24–36 h after treatment. Numbers of organisms had recovered by 4 wk to 3 mo after treatment in studies by Maki et al. (1975c) and Maki (1974). Torblaa (1968) found that numbers of organisms in most of his study streams recovered within 6 wk after treatment. Although some species of invertebrates may be substantially reduced in numbers by stream treatments with TFM, it is doubtful that the total biomass of food organisms would be reduced enough to affect the nontarget fishes appreciably.

TFM–Bayer 73

Stream Treatments

The combination of TFM and Bayer 73 (commonly called TFM-2B) has been used since 1963 for the treatment of some streams. Bayer 73 is used in a wettable powder with 70% active ingredient. Smith et al. (1974) report that the amount of Bayer 73 applied is usually 1–2% of the amount of TFM applied, and that this generally reduces the amount of TFM needed by about 50%. The use of Bayer 73 with TFM complicates both the logistics of a stream treatment and the analysis for lampricides. Bayer 73 is also more difficult to apply because of its low solubility and tendency to plug small pumps. Consequently, use of the combination is generally restricted to large rivers where a substantial saving in the amount of chemical needed offsets the added difficulty of the treatment. Bayer 73 is usually added to a stream at the same site or sites as TFM, but in some past treatments, Bayer 73 was added at a point downstream from the TFM application site to boost the activity of TFM already in the stream.

Factors Affecting Toxicity

Toxicity of TFM-2B follows approximately the same pattern as that of TFM alone. Water temperature does not significantly affect toxicity of TFM-2B to fish (Dawson et al. 1977). Dawson et al. (1977) also found no significant effect of water hardness on the toxicity of the combination, but Howell et al. (1964) reported TFM-2B to be more toxic in soft water with low pH than in harder water with higher pH. Probably in the tests by Howell et al. (1964), pH was the influencing factor, but the two factors were not isolated in the test procedure. Dawson et al. (1977) found that high pHs decreased the toxicity of TFM-2B to larval sea lampreys.

The addition of Bayer 73 to TFM results in greater increases in toxicity to sea lampreys than to most of the invertebrates for which laboratory data are available. The safety index (LC50 for invertebrate/LC50 for sea lampreys) for most invertebrates tested is slightly greater for TFM-2B than for TFM alone (Table 2).

Table 2. Safety indices for selected nontarget organisms when exposed to the lampricides TFM and TFM-2B in laboratory tests.

	Safety index[a]	
Organism	TFM[b]	TFM-2B[c]
Gastropoda *Physa* sp.	>11	2.5
Pelecypoda	4.0	6.0
Turbellaria	1.9	1.9
Hirudinea	3.9	5.1
Plecoptera	10.7	19.7
Ephemeroptera *Hexagenia* sp.	2.8	5.1
Simuliidae	2.8	4.4

[a] Twenty-four-hour LC50 for nontarget organism/24-h LC50 for larval sea lamprey.

[b] Estimated from the data of Smith (1967).

[c] Calculated from the data of Rye and King (1976).

Types of Studies

Studies on effects of TFM-2B have been much more limited than those with TFM alone. Rye and King (1976) conducted laboratory bioassays with TFM-2B against a variety of invertebrate organisms (Table 3). Inasmuch as this study was conducted in the same facility with the same water source as the tests with TFM conducted by Smith (1967), these two studies provide the best available data for comparison of the toxicities of the two lampricides to invertebrates.

Sampling by Torblaa (1968) in one stream treated with the combination provided the only field data on the effects of TFM-2B on invertebrates. Three Mile Creek was treated with 5 mg/L of the combination (4.9 mg/L TFM:0.1 mg/L Bayer 73). Treatment summaries on effects of TFM-2B on nontarget organisms were scant because the combination was used in only a small percentage of treatments, and observations have not been routinely recorded in recent years.

Effects on Invertebrates

Aquatic worms — Laboratory tests show turbellarians to be sensitive to TFM-2B (Rye and King 1976; Table 3) and to have the same safety factor as with TFM alone (Table 2). Aquatic annelids are also sensitive to the combination with 24-h LC50 values ranging from 2.2 mg/L for *Tubifex* to 5.2 mg/L for *Lumbriculus* (Rye and King 1976). The laboratory toxicity data indicate that all of the groups of aquatic worms are probably susceptible to mortalities during stream treatments. Torblaa (1968) noted a reduction in annelids from 3 to 0 per square foot (0.092 m²), but

TABLE 3. Toxicity of TFM-2B (98% TFM and 2% Bayer 73) and Bayer 73 to selected macroinvertebrates and larval sea lampreys in laboratory tests. (Data adapted from Rye and King 1976.)

Organism	24-h LC50 and 95% confidence interval (mg/L) TFM-2B	Bayer 73
Gastropoda		
Physa sp.	1.93 (1.54–2.41)	0.106 (0.097–0.116)
Pleurocera sp.	9.4 (7.74–11.4)	0.335 (0.290–0.430)
Pelecypoda		
Elliptio dilatatus	4.7 (3.5–6.3)	0.382 (0.320–0.458)
Turbellaria		
Dugesia tigrina	1.5 (1.42–1.58)	0.048 (0.044–0.053)
Oligochaeta		
Tubifex tubifex	2.25 (1.98–2.55)	0.034 (0.031–0.037)
Lumbriculus inconstans	5.2 (4.8–5.6)	0.14 (0.12–0.18)
Hirudinea		
Erpobdellidae	4.0 (3.3–4.9)	0.42 (0.38–0.47)
Cladocera		
Daphnia pulex	7.35 (5.74–9.41)	0.8 (0.68–0.94)
Isopoda		
Asellus militaris	31.0 (28.7–33.5)	23.0 (18.4–28.8)
Amphipoda		
Gammarus sp.	26.0 (24.4–27.7)	2.6 (2.34–2.88)
Decapoda		
Orconectes sp.	>100	>50
Ephemeroptera		
Hexagenia sp.	4.0 (3.6–4.5)	6.9 (5.85–8.14)
Stenonema sp.	30.5 (26.1–35.7)	2.27 (1.68–3.08)
Odonata		
Ophiogomphus sp.	>100	>50
Plecoptera		
Paragnetina sp.	15.4 (12.4–19.0)	1.07 (0.79–1.44)
Hemiptera		
Corixidae	40.0 (32.8–48.8)	>50
Megaloptera		
Corydalus sp.	>100	>50
Trichoptera		
Hydropsyche sp.	30.0 (25.6–35.1)	2.45 (1.88–3.19)
Helicopsyche sp.	48.0 (38.1–60.5)	1.67 (1.18–2.37)

TABLE 3 (*Concluded*)

Organism	24-h LC50 and 95% confidence interval (mg/L) TFM-2B	Bayer 73
Diptera		
Simulium sp.	3.45 (3.05–3.89)	0.255 (0.236–0.275)
Atherix sp.	>100	>50
Cyclostomata		
Petromyzon marinus	0.78 (0.684–0.889)	0.049 (0.043–0.056)

the very small numbers do not permit conclusions. Dead leeches were noted in the treatment summary of one stream treated with the combination.

Crustaceans — The cladoceran *Daphnia pulex* was moderately sensitive to the combined lampricides. A safety factor of 9.4 in comparison to that of larval lampreys indicates that *Daphnia* would rarely be subjected to lethal concentrations.

Macrocrustaceans were highly resistant to the combination in laboratory tests; 24-h LC50s ranged from 26 mg/L for amphipods to over 100 mg/L for crayfish (Table 3). In Three Mile Creek, Torblaa (1968) observed a 49% reduction in amphipod numbers 1 wk after treatment. Considering the laboratory LC50 of 26 mg/L, the apparent reduction was more likely due to sampling variation or drift than to mortality.

Aquatic insects — Aquatic insects follow a pattern of sensitivity to TFM-2B similar to that of TFM alone, although a comparison of laboratory studies by Rye and King (1976) and Maki et al. (1975a) showed that fewer insects are likely to be affected by TFM-2B. Rye and King (1976) showed that burrowing mayflies and black flies were the only organisms likely to be affected by stream treatments with TFM-2B. Numbers of these organisms in the field samples taken by Torblaa (1968) were too small to permit conclusions. Torblaa (1968) showed a 94% reduction in numbers of caddis flies of the family Psychomyiidae. Since the number of species within families were limited in the tests by Rye and King (1976), some sensitive species may exist within generally resistant families as was shown for TFM by Maki et al. (1975a). The safety indices for mayflies and black flies are 4–5 (Table 2), while those for other insects tested are over 19, indicating that few taxa of insects are likely to be exposed to lethal concentrations of TFM-2B.

Molluscs — Published data on the effects of TFM-2B on molluscs are limited to laboratory tests of two genera of snails and one of clams (Rye and King 1976). *Physa* is very sensitive but *Pleurocera* is more resistant and not likely to be affected by stream treatments (Table 3).

The clam *Elliptio dilatatus* was quite sensitive to the combination (Table 3); however, no mortalities of clams have been reported in streams treated with TFM-2B.

EFFECTS ON VERTEBRATES

No quantitative data are available on the effects of TFM-2B on aquatic vertebrates other than fish. The treatment summaries for the Tahquamenon River (Michigan) included observations on dead mud puppies in 3 different years. Since mortalities of mud puppies are common in streams treated with TFM alone, a similar frequency of mortalities is probable with TFM-2B.

OVERALL EFFECTS OF TFM-2B TREATMENTS

Only limited data are available on effects of TFM-2B on invertebrates. The laboratory test data indicate that aquatic worms (turbellarians and annelids), burrowing mayfly nymphs, black fly larvae, some snails, and some clams are likely to be affected. In addition, field observations show mortalities of mud puppies. The overall effects of treatments with TFM-2B on invertebrates are probably less than those with TFM alone, because the addition of Bayer 73 to TFM increased the toxicity to sea lampreys to a greater degree than for most invertebrates.

Granular Bayer 73

TREATMENTS

Granular Bayer 73 (5% active ingredient) is used to treat populations of larval lampreys in lentic areas near the mouths of streams in which sea lampreys spawn. The material is applied to areas up to several hectares in size with a gasoline-powered blower or a cyclone-type spreader, usually from a boat. Amounts of the formulation used are usually 112–168 kg/ha (100–150 lb/acre) in the United States and 224 kg/ha in Canada. Such applications are intended to deliver a theoretical concentration of active ingredient in the bottom 5 cm of water of 11.5–17.2 mg/L in U.S. treatments and 23 mg/L in Canadian treatments. However, laboratory tests have shown that even under ideal conditions of temperature and pH of the water, less than 40% of the active ingredient is released over a period of 24 h (U.S. Fish and Wildlife Service, National Fishery Research Laboratory, La Crosse, Wisconsin, unpublished data). Usually within an hour after application, larval lampreys emerge from their burrows in the bottom sediments and swim to the surface of the water, where they can be observed or collected. Some measure of control is accomplished during such surveys because many of the larvae have received a lethal dose by the time they leave their burrows (Tibbles 1967).

FACTORS AFFECTING TOXICITY

Dawson et al. (1977) conducted laboratory tests on Bayer 73 under varied water conditions using both larval sea lampreys and fish as test organisms. They found a slight reduction in toxicity at lower temperatures. Field application crews have reported that the time required for the chemical to drive lampreys to the surface is much increased at temperatures below 10°C. Water hardness had no measurable effect on toxicity over a range of 44–800 mg/L total hardness. Dawson et al. (1977) found that Bayer 73 was somewhat more toxic at low pH than at high pH, but this effect was not great over the range of pH found in most of the lamprey-producing waters (7.5–8.5). The general conclusion indicated by laboratory tests on fish is that water chemistry has little effect on the toxicity of the chemical. Tests on invertebrates have not included variations in water chemistry.

TYPES OF STUDIES

Bayer 73 has been studied and used as a control for snail vectors of schistosomiasis in tropical countries and for control of larval sea lampreys in the U.S. Laboratory and field studies have been conducted in the tropical countries on the effects of Bayer 73 on snails and nontarget invertebrates. In the U.S., small-scale laboratory tests have been done with algae (Farringer 1972) and aquatic invertebrates (Sanders 1977). Rye and King (1976) did a comprehensive laboratory study which included larval lampreys for comparison with invertebrates (Table 3).

Laboratory studies that establish 24-h LC50s, however, do not necessarily approximate the effects of Bayer 73 as it is used in lamprey surveys. The treatments are designed to establish a high concentration for a brief period of time with the assumption that the chemical will quickly be diluted by the surrounding water. Field observations indicate that the activity of the chemical usually lasts less than 2 h against larval lampreys.

Effects of Bayer 73 on invertebrates under natural conditions were assessed by personnel at Hammond Bay Biological Station, Millersburg, Michigan (unpublished data) in treatment of a small plot in the Ocqueoc River (Michigan) at a rate of 18.8 kg/ha (active ingredient). Only one quantitative field study of the effects of granular Bayer 73 on invertebrates in lentic areas has been done (Gilderhus 1979). In that study, samples were taken up to 13 d after treatment of a 0.8-ha plot in Boardman Lake (Michigan) at a concentration of 11.5 mg/L in the bottom 5 cm of water.

EFFECTS ON PLANTS

Farringer (1972) found that high concentrations (50 mg/L) of Bayer 73 affected algae (*Chlamydomonas* and *Chlorella*) by reducing their growth by 50% over a period of 8 d. Interpolation of these results to the much lower concentrations and shorter exposure times required in lamprey surveys indicates that little effect on algae would be expected in treatment of lentic areas. Shiff and Garnett (1961) observed a severe setback of *Chara* by 1 mg/L of Bayer 73 in ponds. In contrast, Abdalla and Nasr (1961) found that concentrations up to 5 mg/L did not harm aquatic vegetation. Considering the type of treatment used in the lamprey control program, it is unlikely that vegetation would be noticeably affected.

EFFECTS ON INVERTEBRATES

Aquatic worms — Rye and King (1976) showed that aquatic worms are very sensitive to Bayer 73 at concentrations far below those used in lentic habitat (Table 3). As expected in the field, numbers of oligochaetes and leeches were reduced by 80–90% after treatment (Gilderhus 1979).

Crustaceans — Microcrustaceans are very sensitive to Bayer 73. Pond studies showed reductions of cladocera, copepods, and ostracods after treatments at 1 mg/L, but populations returned to normal within 32 d (Shiff and Garnett 1961). An LC50 of 23 mg/L for isopods (Rye and King 1976) indicates that they are not likely to be affected by field treatments. Amphipods are more sensitive; published 24-h LC50s have ranged from 2.6 mg/L (Rye and King 1976) to 5.6 mg/L (Sanders 1977). Considering the low LC50 values for amphipods, some mortality would be expected from field use of Bayer 73. However, there was no reduction in the substantial population of amphipods present in the study by Gilderhus (1979).

Crayfish are highly resistant, having 24-h LC50 values of 32 mg/L (Sanders 1977) to over 50 mg/L (Rye and King 1976).

Aquatic insects — Aquatic insects vary greatly in their resistance to Bayer 73. Some, such as dragonfly nymphs, water boatmen, snipe fly larvae, and dobsonfly larvae are highly resistant; 24-h LC50s exceed 50 mg/L (Rye and King 1976). Others, including some of the important fish food groups, have 24-h LC50 values in the range of 1–10 mg/L. Laboratory LC50 data cannot be easily used to estimate effects in the field because in operational treatments the organisms are exposed to much higher concentrations for much shorter periods of time.

Stonefly nymphs are sensitive to Bayer 73; 24-h LC50s range from 1.1 to 2.3 mg/L (Sanders and Cope 1968; Rye and King 1976). However, stoneflies are not likely to be present in lentic habitats.

Mayfly nymphs were moderately sensitive in laboratory tests (Table 3). King (1974) listed an LC50 for mayflies of 11.4 mg/L. No effect was found on a substantial population of mayflies following a field treatment of 11.5 mg/L (Gilderhus 1979).

Caddis flies also were sensitive to Bayer 73 in laboratory tests (Table 3). An experimental treatment in the Ocqueoc River reduced the caddis fly larvae population by about 90% (Hammond Bay Biological Station, unpublished data). The treatment in Boardman Lake showed a 40% reduction in numbers of caddis fly larvae at 7 d after treatment (Gilderhus 1979).

Beetle larvae were not included in any laboratory tests and no field data are available.

In contrast to snipe flies, some of the Diptera are very sensitive to Bayer 73. Black flies (Table 3) were virtually eliminated by an 18.8 kg/ha treatment in the Ocqueoc River (Hammond Bay Biological Station, unpublished data). However, black flies are not likely to inhabit the lentic areas treated with granular Bayer 73.

Midge larvae (*Chironomus*) are also sensitive. Kawatski et al. (1975) showed that 50% of the organisms were immobilized by 0.6–0.8 mg/L in 24-h laboratory tests. Gilderhus (1979) found that numbers of midge larvae were reduced by a statistically significant 54% at 7 d after treatment in Boardman Lake.

Molluscs — Molluscs are very sensitive to Bayer 73 (Table 3). Abdalla and Nasr (1961) killed all snails (*Bulinus*) with 1 mg/L in 4 h and 2 mg/L in 2 h in laboratory tests. In field applications in Egypt, Abdalla and Nasr (1961) found that applications of 1 mg/L for 5 h gave 100% control of snails (*Bulinus* and *Biomphalaria*) in standing water, and 1 mg/L for 8 h gave complete control in flowing water. Harrison (1966) reported that blanket spraying of two streams in Rhodesia at 0.2–0.4 mg/L of Bayer 73 killed all snails. After the lamprey treatment in Boardman Lake, Gilderhus (1979) found that snails were essentially unaffected even though the theoretical concentration was much higher than that required to kill snails elsewhere.

Clams are as sensitive as snails in laboratory tests (Table 3) and apparently are more sensitive under field conditions. The plot treatment in the Ocqueoc River reduced the numbers of clams (Hammond Bay Biological Station, unpublished data), and Gilderhus (1979) found a 62% reduction in numbers of clams by 7 d after treatment in Boardman Lake.

Considering the extreme sensitivity of molluscs to Bayer 73 in laboratory tests, adverse effects of field treatments on molluscs were less than expected.

OVERALL EFFECTS OF BAYER 73 TREATMENTS

Effects of Bayer 73 treatments on nontarget organisms in the field were generally less than expected. Aquatic worms (Oligochaeta) and midge larvae were the most sensitive, and significant short-term declines in their populations can be expected. Moderate declines can be expected in numbers of microcrustaceans and molluscs (especially clams). Other organisms, such as amphipods and mayflies, were not affected by the field treatment studied, but may be subject to mortalities from some treatments.

Considering that the use of Bayer 73 for survey or control of sea lamprey larvae in lentic habitat will involve only a small percentage of any body of water, the effects on invertebrate populations are expected to be minor.

Summary and Discussion

The studies done on the effect of TFM treatments in streams have included a variety of laboratory and field assessments which help evaluate the real and potential impact of this chemical on nontarget organisms. The effects of TFM-2B on invertebrates in laboratory tests seem to be less than those of TFM, but a comprehensive stream study would be needed for confirmation. Work on Bayer 73 for treatment of lentic habitats has not been extensive, but is probably adequate to estimate potential effects in many treatments. However, in the only field study done to date, the treatment rate was 112 kg/ha of the granular formulation, whereas up to twice that amount is used in Canadian treatments. Further field study would be needed to assess adequately effects of higher treatment rates on nontarget organisms.

Maki et al. (1975a) observed that early life stages of some invertebrates were more sensitive than later stages, and species with well developed exoskeletons were most resistant to TFM. Laboratory toxicity tests done on specimens collected in the field and field observations have probably been heavily weighted toward larger specimens or relatively mature life stages. Therefore the available data may underestimate the effect of lampricides on some invertebrates.

The overall impact of lampricides on invertebrates has probably been of minor importance in aquatic ecosystems. Although significant mortalities of some fish food organisms may occur, they are usually confined to small segments of a particular stream system, and other important food organisms are left unaffected. No evidence exists to indicate that a species has been totally eliminated from a stream. In nearly all streams and lakes treated for lampreys, a portion of the system remains untreated to provide organisms for recolonization of the treated area.

The use of almost any toxicant for the control of a pest organism involves nontarget organisms to some degree. The user must therefore evaluate the impact on the ecosystem against the benefit derived from control of the pest or predator organism. The occasional kills of certain nontarget organisms appear insignificant in comparison with the benefit that sea lamprey control affords the fish populations of the Great Lakes.

ABDALLA, A., AND T. S. NASR. 1961. Evaluation of a new molluscicide, Bayer 73. Egypt Med. Assoc. 44: 160–170.

APPLEGATE, V. C., J. H. HOWELL, J. W. MOFFETT, B. G. H. JOHNSON, AND M. A. SMITH. 1961. Use of 3-trifluormethyl-4-nitrophenol as a selective sea lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 1: 35 p.

CHANDLER, J. H. JR., AND L. L. MARKING. 1975. Toxicity of the lampricide 3-trifluoromethyl-4-nitrophenol (TFM) to selected aquatic invertebrates and frog larvae. U.S. Fish Wildl. Serv. Invest. Fish Control 62: 7 p.

DAWSON, V. K., K. B. CUMMING, AND P. A. GILDERHUS. 1975. Laboratory efficacy of 3-trifluoromethyl-4-nitrophenol (TFM) as a lampricide. U.S. Fish Wildl. Serv. Invest. Fish Control 63: 13 p.

1977. Efficacy of 3-trifluoromethyl-4-nitrophenol (TFM), 2′,5-dichloro-4′-nitrosalicylanilide (Bayer 73) and a 98:2 mixture as lampricides in laboratory studies. U.S. Fish Wildl. Serv. Invest. Fish Control 77: 11 p.

FARRINGER, J. E. 1972. The determination of acute toxicity of rotenone and Bayer 73 to selected aquatic organisms. M.S. thesis, University of Wisconsin-La Crosse, WI. 32 p.

FREMLING, C. R. 1975. Acute toxicity of the lampricide 3-trifluoromethyl-4-nitrophenol (TFM) to nymphs of mayflies (*Hexagenia* sp.). U.S. Fish Wildl. Serv. Invest. Fish Control 58: 8 p,

GILDERHUS, P. A. 1979. Effects of granular 2′,5-dichloro-4′-nitrosalicylanilide (Bayer 73) on benthic macroinvertebrates in a lake environment. Great Lakes Fish. Comm. Tech. Rep. 34: 5 p.

HAAS, R. C. 1970. The effects of lamprey larvicide on the bottom fauna and periphyton of the Chocolay River, Marquette County, Michigan. Mich. Dep. Nat. Resour., Res. Dev. Rep. 200: I–VI: 66 p.

HARRISON, A. D. 1966. The effects of Bayluscide on gastropod snails and other aquatic fauna in Rhodesia. Hydrobiologia 28: 371–384.

HOWELL, J. H., E. L. KING, A. J. SMITH, AND L. H. HANSON. 1964. Synergism of 5,2′-dichloro-4′-nitro-salicylanilide and 3-trifluormethyl-4-nitrophenol in a selective lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 8: 21 p.

JOSEPHS, M. J. 1961. Control of aquatic plants. U.S. Patent 3,004,843. Filed August 10, 1959, patented October 17, 1961. 3 p.

KAWATSKI, J. A., M. M. LEDVINA, AND C. R. HANSEN JR. 1975. Acute toxicities of 3-trifluoromethyl-4-nitrophenol (TFM) and 2′,5-dichloro-4′-nitrosalicylanilide (Bayer 73) to larvae of the midge (*Chironomus tentans*). U.S. Fish Wildl. Serv. Invest. Fish Control 57: 7 p.

KING, E. L. JR. 1974. Toxicity of Bayluscide to larval sea lampreys, rainbow trout and mayfly nymphs, p. 21. *In* U.S. Bureau of Sport Fisheries and Wildlife, Fish Control Laboratory, Southeastern Fish Control Laboratory, and Hammond Bay Biological Station, Annual Report for 1973. National Fishery Research Laboratory, La Crosse, WI.

MAKI, A. W. 1974. The effects and fate of lampricide (TFM:3-trifluoromethyl-4-nitrophenol) in model stream communities. Ph.D. thesis, Michigan State University, East Lansing, MI. 162 p.

MAKI, A. W., L. GEISSEL, AND H. E. JOHNSON. 1975a. Comparative toxicity of larval lampricide (TFM:3-trifluoromethyl-4-nitrophenol) to selected benthic macroinvertebrates. J. Fish. Res. Board Can. 32: 1455–1459.

1975b. Toxicity of the lampricide 3-trifluoromethyl-4-nitrophenol (TFM) to 10 species of algae. U.S. Fish Wildl. Serv. Invest. Fish Control 56: 17 p.

1975c. Effects of experimental lampricide treatments on the community structure of benthic macroinvertebrates in Cheney Creek, Paris, Michigan. Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI. 11 p.

MAKI, A. W., AND H. E. JOHNSON. 1976. Evaluation of a toxicant on the metabolism of model stream communities. J. Fish. Res. Board Can. 33: 2740–2746.

1977. The influence of larval lampricide (TFM:3-trifluoromethyl-4-nitrophenol) on growth and production of two species of aquatic macrophytes, *Elodea canadensis* (Michx.) planchon and *Myriophyllum spicatum* L. Bull. Environ. Contam. Toxicol. 17: 57–65.

MARKING, L. L., AND L. E. OLSON. 1975. Toxicity of the lampricide 3-trifluoromethyl-4-nitrophenol (TFM) to nontarget fish in static tests. U.S. Fish Wildl. Serv. Invest. Fish Control 60: 13 p.

RYE, R. P. JR., AND E. L. KING JR. 1976. Acute toxic effects of two lampricides to twenty-one freshwater invertebrates. Trans. Am. Fish. Soc. 105: 322–326.

SANDERS, H. O. 1977. Toxicity of the molluscicide Bayer 73 and residue dynamics of Bayer 2353 in aquatic invertebrates. U.S. Fish Wildl. Serv. Invest. Fish Control 78: 7 p.

SANDERS, H. O., AND O. B. COPE. 1968. The relative toxicities of several pesticides to naiads of three species of stoneflies. Limnol. Oceanog. 13: 112–117.

SANDERS, H. O., AND D. F. WALSH. 1975. Toxicity and residue dynamics of the lampricide 3-trifluoromethyl-4-nitrophenol (TFM) in aquatic invertebrates. U.S. Fish Wildl. Serv. Invest. Fish Control 59: 9 p.

SHIFF, C. J., AND B. GARNETT. 1961. The short term effects of three molluscicides on the microflora and microfauna of small biologically stable ponds in southern Rhodesia. Bull. WHO 25: 543–547.

SMITH, A. J. 1967. The effects of the lamprey larvicide, 3-trifluoromethyl-4-nitrophenol on selected aquatic invertebrates. Trans. Am. Fish. Soc. 96: 410–413.

SMITH, B. R., AND R. A. BRAEM. 1976. Lamprey control in the United States, Appendix V, p. 153–181. *In* Great Lakes Fishery Commission, Report of annual meeting, Traverse City, MI, June 15–16, 1976.

SMITH, B. R., J. J. TIBBLES, AND B. G. H. JOHNSON. 1974. Control of the sea lamprey (*Petromyzon marinus*) in Lake Superior, 1953–70. Great Lakes Fish. Comm. Tech. Rep. 26: 60 p.

TIBBLES, J. J. 1967. Lamprey control experiment in Canada, p. 41–46. *In* Great Lakes Fishery Commission annual report for 1966.

TORBLAA, R. L. 1968. Effects of lamprey larvicides on invertebrates in streams. U.S. Fish Wildl. Serv. Spec. Sci. Rep.-Fish. 572. 13 p.

Adult Biology of the River Lamprey (*Lampetra ayresi*) and the Pacific Lamprey (*Lampetra tridentata*) from the Pacific Coast of Canada

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BEAMISH, R. J. 1980. Adult biology of the river lamprey (*Lampetra ayresi*) and the Pacific lamprey (*Lampetra tridentata*) from the Pacific coast of Canada. Can. J. Fish. Aquat. Sci. 37: 1906–1923.

River lamprey (*Lampetra ayresi*) metamorphose in late July with downstream migration occurring in the following year from May to July. Once adults enter salt water they begin to feed immediately by consuming chunks of flesh primarily from herring and young salmon. From June until September they increase in size by an estimated 11–14 cm and 12–18 g. In 1975, 667 000 lamprey were estimated to be in the Strait of Georgia resulting in the deaths of 60 000-000 juvenile fish. Between September and late winter river lamprey return to freshwater. Spawning occurs in the spring, from April to June and adults die after spawning. The length of adult life from the onset of metamorphosis until death following spawning is 2 yr. Pacific lamprey (*Lampetra tridentata*) begin metamorphosis in July and the known period of entry into salt water is from December until June. Feeding can commence in freshwater or salt water by mid-October. Pacific lamprey move into water deeper than 20–70 m and are present in all major fishing grounds off Canada's west coast. A relatively high incidence of lamprey attacks has been observed on sockeye and pink salmon that are aggregating in preparation to return to freshwater. The smallest mature or maturing pacific lamprey found in this study measured 16 cm and the largest measured 72 cm. Adults may spend 3½ yr in salt water before returning to freshwater from April to June and completing their upstream migrations by late September. Stocks that return in the spring exhibit exceptional migratory instincts often migrating considerable distances in freshwater to the uppermost regions of tributary streams before they spawn from April to July in the following year. After entry into freshwater and prior to spawning, adults shrink in length by approximately 20%. The average life span from the onset of metamorphosis until death following spawning probably is 5 yr. A nonanadromous form that appears to be a new species exists in lakes and attacks a large percentage of resident salmonids.

Key words: Pacific lamprey, river lamprey, life history, fish parasites, Pacific fishes

BEAMISH, R. J. 1980. Adult biology of the river lamprey (*Lampetra ayresi*) and the Pacific lamprey (*Lampetra tridentata*) from the Pacific coast of Canada. Can. J. Fish. Aquat. Sci. 37: 1906–1923.

La métamorphose de la lamproie fluviatile américaine (*Lampetra ayresi*) a lieu fin juillet, la migration en aval se produisant de mai à juillet de l'année suivante. Aussitot arrivés en eau salée, les adultes commencent à se nourrir de morceaux de chair arrachés en grande partie à des harengs et de jeunes saumons. De juin à septembre, les lamproies croissent d'environ 11 à 14 cm et 12 à 18 g. On avait estimé en 1975 qu'il y avait 667 000 lamproies dans le détroit de Géorgie, entraînant la mort de 60 millions de jeunes poissons. Les lamproies fluviatiles américaines retournent en eau douce entre septembre et la fin de l'hiver. La fraie a lieu au printemps, d'avril à juin, après quoi les adultes meurent. La durée de vie adulte, depuis le début de la métamorphose jusqu'à la mort suivant la fraie, est de 2 ans. La lamproie du Pacifique (*Lampetra tridentata*) commence à se métamorphoser en juillet et, en autant qu'on le sache, pénètre en eau salée de décembre à juin. Elle peut commencer à se nourrir en eau douce ou en eau salée vers la mi-octobre. Les lamproies du Pacifique se dirigent vers des eaux de profondeur dépassant 20 à 70 m et sont présentes sur tous les principaux lieux de pêche du large de la côte occidentale canadienne. On a observé une incidence relativement haute d'attaques de lamproies sur des saumons nerka et roses réunis en bancs avant leur retour en eau douce. La plus petite lamproie mature ou en voie de maturation rencontrée dans la présente étude mesurait 16 cm, et la plus grande 72 cm. Les adultes peuvent passer 3½ ans en eau salée avant

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de retourner en eau douce entre avril et juin, cette migration en amont étant terminée fin septembre. Les stocks qui retournent au printemps exhibent des instincts migrateurs exceptionnels, parcourant souvent des distances considérables en eau douce pour atteindre les régions supérieures des cours d'eau tributaires avant de frayer entre avril et juillet de l'année suivante. Après leur entrée en eau douce et avant la fraie, les adultes rapetissent d'environ 20%. La durée de vie moyenne, depuis le début de la métamorphose jusqu'à la mort suivant la fraie, est probablement de 5 ans. Une forme non anadrome, apparemment une espèce nouvelle, existe dans les lacs et attaque un fort pourcentage de salmonidés résidents.

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Two species of parasitic lampreys are found off Canada's west coast. Very little is known about the biology of the Pacific lamprey (*Lampetra tridentata*) and almost nothing is known about the biology of the river lamprey (*Lampetra ayresi*). The purpose of this report is to present new information about the adult phase of the life cycle of these two species, including a description of metamorphosis and spawning.

Materials and Methods

Collections were obtained in freshwater using electroshockers, fish weirs that trapped fish moving downstream and occasionally upstream, purse seines, and small midwater trawls. In salt water, samples were obtained using purse seines with small mesh, plankton nets, and large commercial-size midwater trawls with small mesh liners in the codend. Lamprey maintained in the laboratory were held in a variety of tanks ranging in size from 800 to 4250 L. Salt water was obtained directly from the Strait of Georgia and the salinity ranged from 27 to 30‰ annually. Freshwater was dechlorinated city of Nanaimo water. Except for an experiment to induce river lamprey to spawn, no attempt was made to regulate temperature. Lamprey in the laboratory tanks were fed on a variety of species of fishes but primarily Pacific herring (*Clupea harengus pallasi*) and sockeye salmon (*Oncorhynchus nerka*). Ammocoetes were fed 200 mL of dry yeast suspension (200 cm^3 of brewers yeast in 1 L) twice a week (Hanson et al. 1974). Adult river lamprey gut contents were examined in the laboratory by recovering the entire gut content, measuring the volume and examining the contents with a microscope. All weights of live specimens were determined after lampreys were anesthetized in MS-222. All lengths are total lengths and were made using fresh specimens unless indicated. Additional details of most methods are described in Beamish and Williams (1976) and Beamish and Scarsbrook (1979). When appropriate, special comments about methodologies will be included in the descriptions of the life histories.

IDENTIFICATION OF ADULTS

The tooth pattern clearly separates adult Pacific lamprey from the river lamprey and the western brook lamprey (*L. richardsoni*). River lamprey in salt water can also be identified by the lighter color, presence of countershading, and less robust appearance. However, separation of metamorphosing stages of river and western brook lamprey was not possible as recently metamorphosed western brook lamprey have rather prominent cusps and a dentition pattern similar to the parasitic river lamprey. Confirmation of the identity of some western brook lampreys was obtained by holding recently metamorphosed adults over winter in freshwater, and confirming that they matured and in some cases spawned in the early spring of the year following metamorphosis. Characters that will enable the separation of these two species during the macrophthalmia stage have not been identified because up to the present all but two of the recently metamorphosed specimens, captured in the fall and tentatively identified as river lamprey, proved to be western brook lamprey. Therefore, at present, the separation of metamorphosed river and western brook lamprey from samples collected in the fall remains uncertain.

In the spring, immature adult river lamprey in freshwater can be distinguished, in most cases, by the silver color of the body, the prominence and sharpness of teeth, the immature state of the gonads and the advanced state of development of the gut. In the late fall and early spring, river lamprey returning from sea and found in freshwater can be separated from recently transformed western brook lamprey by their advanced stage of maturity and the sharpness of their teeth.

At present, the identification of ammocoetes of river and western brook lamprey are also in doubt. Identifications of ammocoetes were made according to original published descriptions (Pletcher 1963; Vladykov and Follett 1958, 1965); however, not one of the ammocoetes thought to be a river lamprey developed into a river lamprey in the holding tanks.

In some streams adult lamprey were found that possessed characteristics common to both river lamprey and western brook lamprey. These lamprey were silver and possessed a well-defined gut, but the gonad development although more advanced than samples of river lamprey from other streams, was much less advanced than western brook lamprey found in the same stream. Two of these forms died when an attempt was made to acclimate them to salt water. There also was some variation in the morphology of western brook lamprey. Comparative studies of eye diameters, prebranchial lengths, and the number and morphology of velar tentacles confirmed that there are important variations in river and western brook lampreys found in the various rivers.

Results and Discussion

BIOLOGY OF ADULT RIVER LAMPREY

Since ammocoetes and recently metamorphosed river lamprey could not be separated from western brook lamprey, it could only be assumed that river lamprey ammocoetes begin metamorphosis in July, at the same time as the other two species. River lamprey have been

TABLE 1. Length frequency of juvenile adult river lamprey caught in downstream traps, in three British Columbia rivers.

Length (cm)	Fraser River[a] June 6–9, 1978	Fraser River[a,b] April 24–June 5, 1979	Morrison Creek[b] May 20–June 11, 1978	Quinsam River[b] April 26, 1978
4	1	—	—	—
5	—	—	—	—
6	—	—	—	—
7	—	—	—	—
8	—	—	—	—
9	3	6	—	—
10	28	23	—	1
11	28	56	4	—
12	15	76	8	—
13	4	31	5	—
14	—	6	—	—
15	—	2	—	—
16	—	1	—	—
17	—	—	—	—
18	—	—	—	—
19	—	1	—	—
Total	79	202	17	1

[a] Samples from 2.5 m^2 small-mesh midwater trawls fished at depths from 0 to 6 m and 3 to 20 km from the mouth of the river. Lengths from samples in 1978 were from previously frozen specimens.

[b] Lengths from preserved samples.

recorded moving downstream from the end of April to mid-June in three rivers in British Columbia. The length of the downstream migrants ranged from 4 to 19 cm with a mean length of 11 cm (Table 1). In 1979, small mesh midwater trawls were fished in the Fraser River starting March 13–16 but river lamprey were not captured until the end of April. Sampling continued until June 5 when the project was terminated because of decreased salmon abundance. While river lamprey occurred in greatest abundance during the last 2 wk of May, they were still present in early June and it is suspected that river lamprey migration into salt water continued throughout June. In 1979, there was no significant difference (t-test, $P > 0.05$) in the mean length of migrants during the main portion of the migration; however, the mean length of the June sample was 0.8 cm smaller than the mean length in the other sampling periods. Most lamprey were found at the 3–6 m depth range in the day samples. Day and night sets were made on May 3 and 17 and while catches were small (9 and 20 river lamprey, respectively), compared to catches during the day, one more river lamprey was captured in the night sets on May 3 and four more in the night sets on May 17 indicating downstream migration continues day and night with a possible preference for the night.

As part of another study, extensive fishing operations using small-mesh surface nets were conducted in the Strait of Georgia in the vicinity of the mouth of the Fraser River from the end of April to mid-July (Robinson et al. 1968a, b; Robinson 1969; Barraclough and Fulton 1967). The earliest recorded catch of river lamprey was on May 4, and catches of river lamprey in the size range of the downstream migrants listed in Table 1 continued to be present in the samples until mid-July, indicating that migration into salt water continued through June and perhaps into early July. A survey of 40 sites among the Gulf Islands in the Strait of Georgia in mid-May 1978 using a small-mesh purse seine (Beamish and Scarsbrook 1979) did not capture any river lamprey. Thus it appears that river lamprey begin to enter salt water late in April or early May and continue moving into salt water possibly as late as early July.

Withler (1955) observed a 162 mm river lamprey feeding on a young coho salmon fingerling in the Skeena River (54°10′N, 130°11′W) in mid-July, 1955. This specimen was larger than most downstream migrants observed in this study and was found in freshwater at about the same time as the maximum abundance of river lamprey was observed in the Strait of Georgia. While migration into salt water may be later for more northern areas, it is possible that the large size and the apparent delayed entry into salt water was related to the initiation of feeding in freshwater.

In June 1976, 50 juvenile sockeye salmon were captured at depths of 190 and 54 m in the northern portion of the Strait of Georgia (Scarsbrook et al. 1980). Seven of these fish had fresh, severe lamprey wounds some of which were identified from the tooth pattern as resulting from river lamprey attacks. The sockeye had an average length of 10 cm and thus had recently entered salt water. Since river lamprey have never been captured in deep water it is probable that

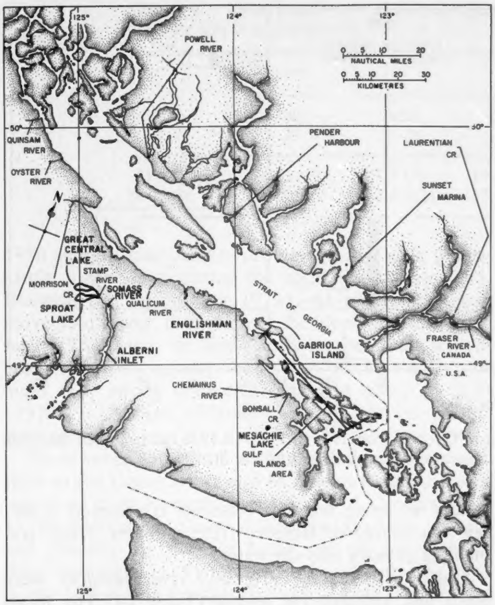
125°
124°
123°
POWELL RIVER
0 5 10 20
NAUTICAL MILES
0 5 10 20 30
KILOMETRES
50°
QUINSAM RIVER
OYSTER RIVER
PENDER HARBOUR
LAURENTIAN CR
SUNSET MARINA
N
GREAT CENTRAL LAKE
STAMP RIVER
MORRISON CR
SOMASS RIVER
SPROAT LAKE
QUALICUM RIVER
ENGLISHMAN RIVER
STRAIT OF GEORGIA
GABRIOLA ISLAND
ALBERNI INLET
FRASER RIVER
CANADA
U.S.A.
49°
CHEMAINUS RIVER
BONSALL CR
MESACHIE LAKE
GULF ISLANDS AREA

FIG. 1. Strait of Georgia showing areas mentioned in this report.

the attacks on the young salmon occurred during the downstream migration or in the estuary. These observations and the observations by Withler (1955) indicate that some river lamprey commence feeding in freshwater.

EARLY ADULT LIFE IN SALT WATER

In this study the earliest catches of adult river lamprey in salt water were made on May 31 and June 2, 1978 in Sunset Marina in Howe Sound just north of the mouth of the Fraser River (Fig. 1). An entire school of fishes was purse seined and a sample estimated to be about one-third of the total school was removed with dip nets. This subsample contained 18 river lamprey, 1009 Pacific herring, 17 northern anchovy (*Engraulis mordax mordax*), and 5 unidentified salmon. A total of 116 herring (11.5%), 2 northern anchovies (11.8%), and one salmon (20%) were wounded from lamprey attacks. Approximately 75% of the wounds were estimated to be sufficiently severe to cause death. There was a disproportionate number of larger herring that had wounds and fresh scars (Fig. 2). This might be the result of a slightly higher survival rate of the larger fish after an attack rather than a preference for large hosts.

After the subsample was removed, an attempt was made to catch the remaining lamprey. A total of 40 lamprey were obtained and the mean length (Fig. 2) was 1 cm larger than the mean length found for the 1978 Fraser River sample (Table 1) indicating that these lamprey started feeding immediately on entry into salt water. The occurrence of actively feeding river lamprey in schools of Pacific herring is commonly observed for several weeks from several areas in the Strait of Georgia at this time of year. Therefore, it appears that some river lamprey begin their parasitic existence in salt water by associating themselves with schools of Pacific herring and voraciously feeding while remaining part of the school.

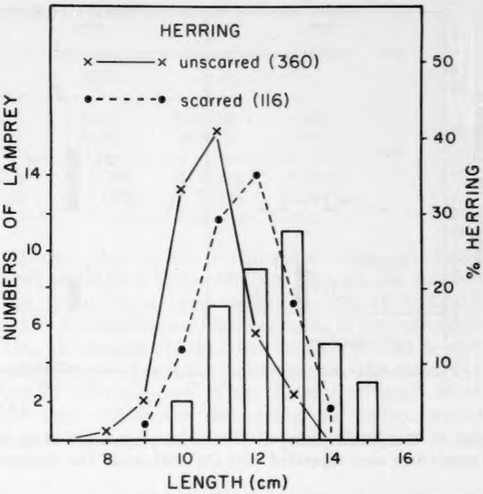

FIG. 2. Length distribution of river lamprey found actively feeding on herring and other fishes in large herring schools in Howe Sound. The length frequency of scarred and unscarred herring is also shown.

GROWTH AND DISTRIBUTION OF ADULTS IN SALT WATER

During 1974, purse seine surveys for river lamprey were conducted in the central portion of the Strait of Georgia during July and August. In 1975 the surveys were repeated and extended into September. In 1976, the effort in the main portion of the Strait of Georgia was reduced but a number of standard locations were fished in the Gulf Islands area (Fig. 1) from April through October. In 1974, 1975, and 1976 the range in length of river lamprey from all the samples was 14–23, 12–29, and 9–28 cm, respectively (Fig. 3). In all years there was a wide range in lengths during July and August with little difference observed among the mean lengths (Fig. 3). The September samples did show an increase in mean length although the number of individuals present in the catch was greatly reduced. The Gulf Islands sample in 1976 does indicate that

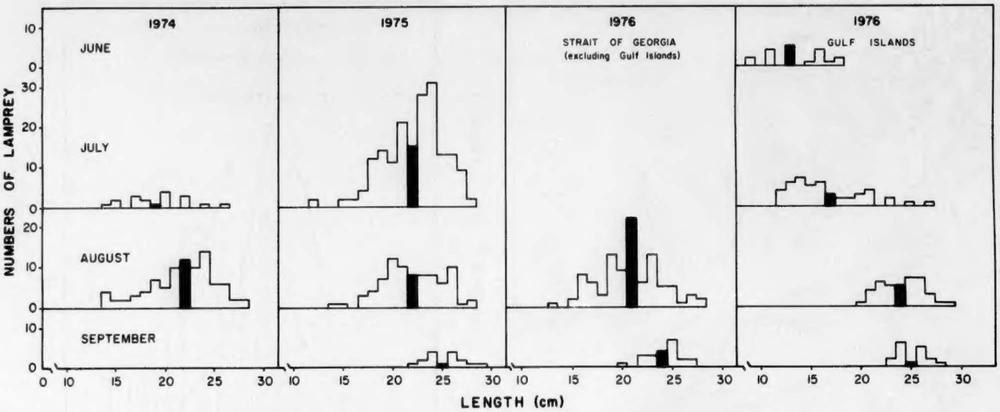

FIG. 3. Length frequency of all river lamprey caught in the Strait of Georgia from 1974 to 1976. In 1976 catches from the Gulf Islands area were separated from the total catch. The shaded bar indicates the mean length of the distribution.

mean length increased from 14 cm in mid-June to 24 cm in mid-August. Increases in length were reduced during late July and August when rapid increases in weight occurred (Fig. 4). The interpretation of growth from length frequencies was complicated by several factors including the time required to complete a survey, the mixing of lamprey from different rivers, and the time of entry into salt water.

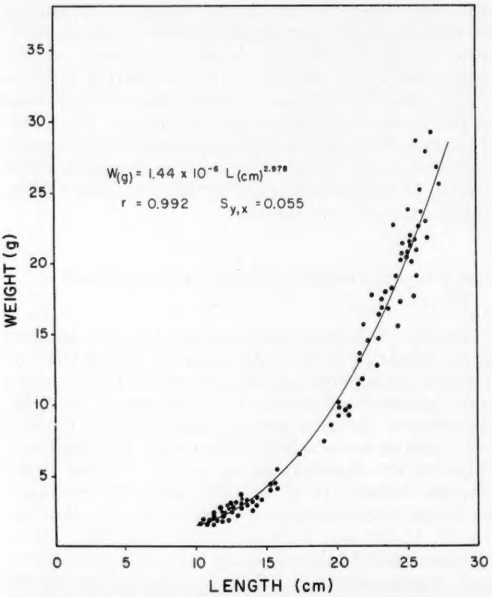

FIG. 4. Relationship between length and weight for adult river lamprey in salt water. The calculated curve does not appear to adequately represent the relationship for length and weight for the largest individuals.

During 1975 and 1976, 229 river lamprey were sexed and sampled for length (Table 2). The mean length of females sampled throughout their salt water residence ranged from being almost identical to being 2.5 cm longer than males. Except for the July 1976 sample there was no significant difference in the mean length of male and female lamprey (t-test, $P > 0.05$).

Sex ratios of adult river lamprey were determined by microscopic examination in 1975 and 1976 when the gut contents were examined. In July 1975 a sample of 50 lamprey consisted of 60% males. In 1976, the sex ratio for the total sample of 182 lamprey examined was 60% females. During July and early August 1976, the ratio of males to females was almost identical. However, in a sample of 59 lamprey collected in late August, there were 64% males and of 17 lamprey found in early September, 74% were females. Thus the adult sex ratios are about equal, but females appear to remain in the surface waters longer.

River lamprey are present in the surface waters from May to September and are most abundant in July. From 1974 to 1979 approximately 500 midwater trawls have been made in the Strait of Georgia at various depths and at various times of the year. While 66 Pacific lamprey were found, only one river lamprey was captured and that was near the surface. (Data are contained in numerous cruise reports, published by the Fisheries and Marine Service, Canada.) Lamprey were most abundant in the surface waters in July and absent after September. No lamprey were found at the surface in the October survey of the Gulf Islands in 1976 or in the 4-day and 4-night purse seine sets made in the Gulf Islands in November 1974. Also a comparison of 20-day and 17-night sets made in the Gulf Islands in

TABLE 2. Mean length (cm) of river lamprey sampled for length and sex in 1975 and 1976. Sample size is in parenthesis.

	1975	1976				
	July 29	June 21–26	July 5–9	Aug. 3–10	Aug. 24– Sept. 2	Sept. 8–15
Male	20.3 (30)	13.9 (6)	15.3 (23)	23.0 (18)	21.8 (21)	24.6 (4)
Female	19.8 (20)	12.0 (12)	17.8 (23)	23.1 (21)	22.7 (38)	25.3 (13)

1976 showed that catches during the day were significantly higher than during the night (*t*-test, $P < 0.05$, Beamish and Scarsbrook 1979). At night some may move into water deeper than the depth of the purse seine (26–33 m), or move inshore, but they seldom occur at depths greater than 50 m during the day or night. The strong countershading first noted by Kan (1975) is further evidence that this species prefers surface waters.

There seems to be little doubt that a few major rivers such as the Fraser River and its tributaries are a major source of river lamprey in the Strait of Georgia (Fig. 1). By dividing the Strait of Georgia into 7-km squares and plotting the average catch per set for each of these squares (Fig. 5) the areas of concentration were in the vicinity of Pender Harbour, Howe Sound, and the area from the mouth of the Fraser River to Gabriola Island and the Southern Gulf Islands area (Fig. 1).

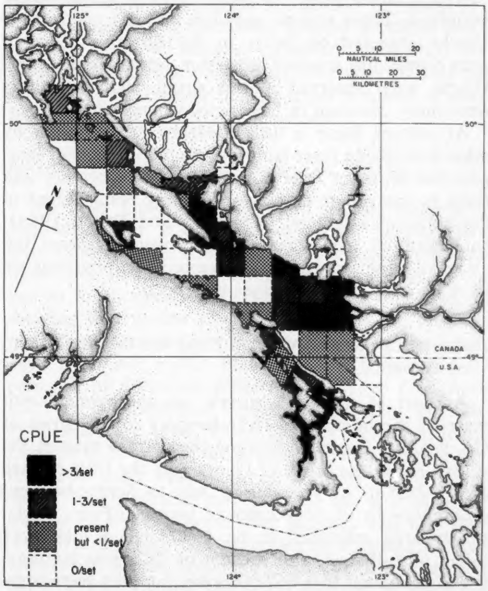

FIG. 5. Catch of river lamprey per unit of effort (CPUE) for all sets made in the Strait of Georgia.

During the summer months the salinity at depths from 10 to 50 m in the Strait of Georgia has an average range of approximately 26–30‰ (Waldichuk 1957). Compared to offshore salinities of approximately 32‰, the salinities in the Strait of Georgia can be considered to be of reduced concentration. The accumulation of river lamprey in the vicinity of major rivers and their distribution throughout the surface waters may indicate a preference for water of reduced salinities.

FEEDING

Gut contents from 182 river lamprey caught in 1976 and from a sample of 50 caught in 1975 were examined in the laboratory. Because river lamprey remove portions of flesh from their hosts (Fig. 6) it was often possible to identify the prey by scales, fin segments, or internal organs such as pyloric caeca. Since much of the gut contents could not be identified, results are expressed as the number of lamprey that contained a particular prey species.

All the identifiable items in each gut were from one prey species. Several guts contained more than one caudal fin or scales from fish of different ages indicating more than one individual had been attacked. Of the 182 guts examined, 38 (22%) were empty and 9 (5%) contained unidentifiable remains. The most frequently occurring species, Pacific herring, was found in 115 (63%) of the guts. Salmon remains were the second most abundant food item occurring in 18 (10%) of the guts. The percent occurrence of salmon remains decreased from 50% in June to 9% in September, while the percent occurrence of herring increased correspondingly. The decrease in the presence of salmon may be related to the movement of young salmon out of the estuaries and the Strait of Georgia. The mean volume of the gut contents was highest in August, averaging 0.8 mL. Because river lamprey often remove pieces of tissue and internal organs, survival of hosts was unlikely. It was estimated from the number of lamprey that contained food, relative to those that were empty, that from June to September each lamprey attacked and fed on 0.8 fish/d.

In laboratory experiments river lamprey fed on a variety of species including Pacific herring, salmonids, shiner perch (*Cymatogaster aggregata*), English sole (*Parophrys vetulus*), on two occasions other river lam-

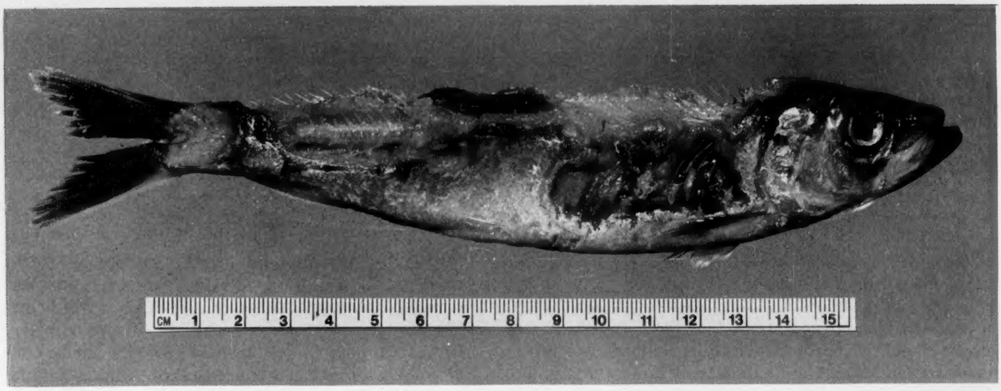

FIG. 6. Pacific herring consumed by river lamprey. The fish was taken from a laboratory feeding experiment and it is apparent from the extensive damage to the body cavity that feeding continued after the death of the host.

prey and one occasion a dead Pacific lamprey. It was not known whether the river lamprey fed on live or dead river lamprey as only a partially consumed carcass was found on the bottom of the tank. On several occasions river lamprey attacked and fed on fish that were already dead. While such attacks were rare, continued feeding on fish that died during an attack was not uncommon. Herring was the preferred species in laboratory experiments and often the addition of fresh herring to a tank would initiate an immediate feeding response. In the laboratory experiments the frequency of feeding was reduced after September. Although river lamprey kept in salt water of the same salinity as the Strait of Georgia started dying in October, those that survived until the following June fed as late as mid-May.

Recreational fishermen have reported that river lamprey attacked their baits and consumed portions of flesh in the length of time it took to retrieve the line. In the laboratory, river lamprey could consume between one-eighth and three-quarters of the body of a small herring (10 cm), exclusive of the head and tail in a single meal of 30–40 min duration. Smaller fish were usually subjected to more general damage with an average of about one-half the trunk tissue being consumed. Larger salmon usually sustained round, deep wounds, often in the anterior dorsal region. Fish smaller than 15 cm seldom survived a lamprey attack for more than a few days or were attacked and killed by another lamprey. During an active 4-wk feeding period in a laboratory experiment, an average of 1.3 fish were killed per lamprey per day (Beamish and Williams 1976). Although it is difficult to relate the results of the number of fish killed in this series of experiments to natural feeding conditions, because lamprey did not feed when first brought into the laboratory, the killing rate of 1.3 fish per lamprey per day is similar to the attacking rate of 0.8 fish per lamprey per day estimated from the analysis of gut contents.

Based on scarring data, Roos et al. (1973) reported that attacks by river lamprey were confined exclusively to the dorsal area. In this study the majority of attacks were dorsal and anterior but some ventral attacks were observed. Ventral attacks probably kill many prey by penetrating the body cavity and would not normally be observed unless large numbers of prey species were examined. There was no question that the majority of attacks observed on fishes in the Strait of Georgia were dorsal, but anterior, posterior, lateral, and ventral attacks were observed in this study. Ventral attacks were more common in laboratory experiments.

At present there is little evidence of predation by other animals on river lamprey. As reported, river lamprey fed on other river lamprey in the laboratory and there is one report of a river lamprey being found in the gullet of a lingcod (Vladykov and Follett 1958). In laboratory experiments in freshwater, salmon fed on small adult western brook lamprey, so predation on river lamprey by other fishes may occur.

ABUNDANCE OF ADULT RIVER LAMPREY IN THE STRAIT OF GEORGIA

As part of the 1975 survey, an approximate estimate of the number of river lamprey in the Strait of Georgia was made by dividing the surface area of the study area in the Strait of Georgia by the total surface area fished in all sets during July to September and multiplying by the total catch of lamprey. From a total survey area estimated to be 4690 km^2, a total area fished of 1.49 km^2, and a catch of 282 river lamprey, it was estimated that 667 000 river lamprey were present in the Canadian portion of the Strait of Georgia (Beamish and Williams 1976). By combining the feed-

TABLE 3. Number of deaths by month for maturing river lamprey held in salt water and freshwater.

	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Total
Salt water												
No. of deaths	4	2	3	1	0	2	1	1	6	2	—	22
(male, female)[a]			(1, 1)			(0, 2)	(1, 0)	(0, 1)	(3, 2)	(2, 0)		
Approximate %	18	9	13	5	0	9	5	5	27	9	—	100
Freshwater												
No. of deaths	—	—	5	9	6	4	3	7	26[b]	6[b]	1[c]	67
(male, female)			(5, 0)	(6, 3)	(4, 2)	(4, 0)	(0, 3)	(1, 1)	(9, 15)	(1, 5)	(0, 1)	
Approximate %	—	—	8	14	9	6	4	10	39	9	1	100

[a] No. of males and females may not add to total as sex was not determined for all fish.

[b] Died after spawning.

[c] Mature female that did not spawn.

ing rate of 0.8 fish per lamprey per day and the killing rate of 1.3 fish per lamprey per day, a killing rate of 1 fish per day per lamprey was assumed. Using this killing rate and assuming that each prey is attacked by only one lamprey it was estimated that 60 000 000 juvenile fish would be killed during the 90-d feeding period from mid-June to mid-September. Since many variables had to be estimated it is obvious that the technique provides only a very approximate estimate of population size. For example, if only the portion of the seine that had a mesh size that could retain lamprey was considered, the effective fishing area would be reduced by 90%. Sets could not always be made in a standard manner in randomly selected locations and it is doubtful that all lamprey remained in the study area during the study period. The estimate does indicate that river lamprey could be an important predator of small fishes particularly herring and salmon.

RETURN TO FRESHWATER, SPAWNING, DEATH

No river lamprey were found in salt water after September, but to date no adult river lamprey have been found in rivers in the fall. Using a small midwater trawl, one maturing 14-cm female river lamprey was caught in Nimpkish Lake on November 30, 1978, indicating that in one river the timing of the upstream migration corresponds with the timing of the disappearance from salt water. Pletcher (1963) recorded the presence of *Lampetra planeri* (now called *L. richardsoni*) in two rivers in British Columbia in February 1957 and May 1942. These lamprey ranged in length from 13 to 20 cm and the largest individuals were larger than any adult western brook lamprey found in this study. It is probable that some of the specimens described by Pletcher were river lamprey and that these were the first recorded observations of maturing river lamprey in British Columbia rivers. Vladykov and Follett (1958) recorded adult river lamprey in San Francisco Bay in the United States in November and February. They also recorded adult river lamprey in Lakes Sammamish and Washington in October and December, respectively. The specimen found in Lake Washington was attached to and possibly feeding on a Kokanee salmon (*Oncorhynchus nerka*). They also reported specimens in spawning condition from the Sacramento River, approximately 240 km from the ocean, in April. From the size of the eggs in these specimens they concluded that the spawning period would be April through May.

In this study, some of the specimens captured in late August and September showed signs of early gonad development. Lamprey held in salt water in the laboratory stopped feeding or fed infrequently after September and died over the period from September to mid-June (Table 3). Individuals that died in November and December were maturing, the gut and eyes were degenerating and there was a noticeable reduction in the postanal length and in the space between the dorsal fins. Such changes are associated with the onset of maturity and onset of upstream migration in other parasitic species (Hardisty and Potter 1971) and suggest that some river lamprey move into freshwater during this time of year. Because a loss of marine osmoregulatory mechanisms occurs with the onset of maturity (Morris 1971), some of the deaths recorded in Table 3 probably are related to changes in osmoregulatory mechanisms. All river lamprey that died in the salt water tanks from February to mid-June were mature. Some river lamprey fed infrequently during this period with the last feeding occurring in mid-May. Although mortalities occurred from September to June, the greatest number occurred in May (Table 3), indicating that some river lamprey can remain in salt water until just before the spawning period. This observation is consistent with that of Vladykov and Follett (1958) who recorded river lamprey in San Francisco Bay at the same time as they were found in some lakes.

In a second experiment, river lamprey were acclimated to freshwater over a period of 6 d in early November and maintained in freshwater. In freshwater,

TABLE 4. Mean length (cm) of Pacific lamprey during metamorphosis and downstream migration (number of fish in sample in parentheses).

	Downstream migrants (trapped)				Metamorphosis adults (electro-shocked)											
	M	A	M	J	J	F	M	A	M	J	J	A	S	O	N	D
Qualicum R. 1977	12 (5)	13 (3)	0	—	—	13 (1)	0	0	0	0	0	—	12 (2)	13 (4)	0	—
Qualicum R. 1978	0	13 (4)	12 (4)	—	—	—	0	0	—	—	—	—	—	—	—	—
Oyster R. 1977	—	—	—	—	—	—	—	—	—	—	—	12 (43)	12 (30)	13 (6)	0	—
Oyster R. 1978	—	—	—	—	—	—	—	—	—	—	—	10 (6)	—	12 (39)	—	—

the pattern of mortalities was similar to that observed for the lamprey held in salt water but by the end of February none of the dead showed advanced signs of maturity and none had fed on any of the salmonids that were kept in the freshwater tanks.

At this time, it can be concluded only that some river lamprey can survive in salt water of approximately 28–30‰ until spawning and that some river lamprey can adapt to freshwater shortly after they disappear from the surface waters in the Strait of Georgia. Separate stocks may exist and some stocks may remain in salt water, possibly in estuaries or below the tide level in rivers during the winter, while others move into lakes and rivers in the fall. Since no spawning occurred in salt water, it appears that a return to freshwater is essential for successful spawning.

River lamprey were acclimated to freshwater in early November 1978, and on April 1, 1979 the water temperature in the tanks was heated to 1–2°C above ambient to correspond with the temperature of rivers known or suspected to contain river lamprey. These lamprey spawned in the holding tanks during May 1979 when the water temperature was 12°C. The nesting and spawning behavior observed in the laboratory was similar to the behavior of most lampreys (Hardisty and Potter 1971). Prior to spawning, lamprey constructed nests approximately 15 cm in diameter in the gravel by lifting rocks out of the nest area with the oral disc and by vigorous digging movements. Just prior to spawning a male would glide up and down the body of the female with his oral disc and eventually attach dorsally behind the head of the female, twisting his tail around the body of the female. The actual release of eggs and sperm was not observed. Males appeared to exert considerable pressure when twisting around the body of females as many spawned females were severely bruised. Most females died within hours of spawning while most males survived for approximately 3 wk.

There was a considerable decrease in length during the period in freshwater from early November until spawning in May. The average length of the 29 spawning lamprey was 18.3 cm. The average length of lamprey in this experiment was 23.8 cm in mid-August and while lengths determined in August were not compared with the length of the same individual measured in May, it is probable that the 21% reduction in length is representative of the amount of shrinkage that occurs during the residence in freshwater prior to spawning. The average length of 14 males was 18.9 cm, about 1 cm longer than the average length of 17.8 cm for 15 females suggesting that females may shrink more than males.

If the temperature at which river lamprey spawned in this study is representative of the temperatures river lamprey initiate spawning in rivers, it can be assumed that most spawning occurs in May and could extend from April to June. Since river lamprey survived only a few weeks after spawning, the average duration of adult life from the onset of metamorphosis in July to death following spawning is 2 yr.

Biology of Adult Pacific Lamprey

METAMORPHOSIS AND MOVEMENT INTO SALT WATER

Metamorphosing Pacific lamprey were first observed in July. Pletcher (1963) also concluded that metamorphosis started in July. Recently an intensive study of the staging of the metamorphosis of Pacific lamprey in the Chemainus River (Richards 1980) confirmed that metamorphosis begins in July and was complete by October. From August to September in the Qualicum River on Vancouver Island (Fig. 1), metamorphosing Pacific lamprey were observed to move from a mud–silt habitat in lentic waters to silt covered large gravel (1 to 4 cm in diameter) in moderate currents. Movement into the large gravel was complete by early September or Stage 6 (teeth blunt, cusps not present on the tongue, oral fimbriae well developed; Richards 1980; Youson and Potter 1979). A survey of other rivers during September, 1979 showed that Pacific lamprey in an advanced stage of metamorphosis characteristically were found in gravel or boulder substrate where currents were moderate to strong. Metamorphosing Pacific lamprey from a nonanadromous population in Mesachie Lake (Fig. 1) were found in similar substrate along the edge of the lake close to the inlet stream.

The mean size of downstream migrants from the Qualicum River was 12.5 cm (Table 4). The mean size of metamorphosing Pacific lamprey, collected from July through to October in the Qualicum and Oyster rivers was 12.0 cm and was not significantly different from the mean size of the total sample of downstream migrants (*t*-test, $P > 0.05$). The average size of eight metamorphosed Pacific lamprey from Morrison Creek was 7.8 cm with the smallest metamorphosed lamprey measuring 4.7 cm. Downstream migrating Pacific lamprey captured with small mesh midwater nets in the Fraser River from May 3 to June 5, 1979 ranged in length from 11 to 16 cm with a mean length of 14 cm for the 43 specimens captured. It appears that, while there is some variation among rivers, the average size of Pacific lamprey when they first enter salt water is approximately 13 cm.

Downstream trapping operations from February to June for salmon often capture lamprey, but unfortunately only in recent years have catches of lamprey been preserved and identified. The earliest reported capture of a juvenile adult Pacific lamprey, moving downstream, was in February (Table 4) and the latest capture was in June, both in the Qualicum River. Unpublished downstream trap catches from the Qualicum River indicate that unidentified lamprey were caught as late as August indicating that the period of migration of Pacific lamprey into salt water may extend past June. In the Fraser River in 1979, no metamorphosed Pacific lamprey were captured in March and April, but 43 were captured in May and June. Pacific lamprey adults are thought to be more abundant than river lamprey adults, yet this number of metamorphosed Pacific lamprey was only 21% of the number of river lamprey caught in the same nets. Because of this apparently small catch of Pacific lamprey it was suspected that the main downstream migration occurred earlier than April and that the catches in May and June resulted from the migration of Pacific lamprey from only a few of the tributary rivers of the Fraser River. The capture of a 12-cm adult Pacific lamprey at a depth of 90 m in December (Fig. 7) in the Strait of Georgia, near the mouth of the Fraser River indicates that migration into salt water can occur at least as early as December. Also, the presence of young adults in areas in the stream with moderate to strong currents, during the periods of low water in September and October suggests that some entry into salt water may occur when water levels and current velocities increase in November. Richards (1980) believed Pacific lamprey go to sea in November.

In a laboratory experiment in 1978, metamorphosing Pacific lamprey were acclimated to salt water in late September and started feeding in mid-October (Richards 1980). This experiment was repeated in late September, 1979 using five metamorphosing Pacific lamprey recently captured from each of five rivers. The stage of metamorphosis was noted and lamprey from each river were marked with an injection of colored latex into the dorsal fin fold. Twenty of the 25 lamprey survived the 3-d period of gradually increasing salinity. The five lamprey that did not survive in full strength salt water were from two rivers and either had not reached stage 6 or had just reached the 6th stage of metamorphosis. None of the lamprey in stage 5 survived in salt water. Live herring (6–10 cm) were added to the tank on October 1 when full strength seawater was achieved. First attachment to a herring was observed in 4 d and the first confirmed feeding on herring occurred in 10 d. By the end of October, 20 herring had been attacked and killed.

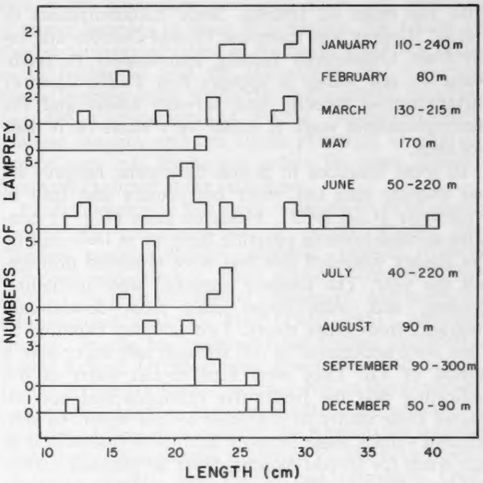

FIG. 7. Length frequency of Pacific lamprey captured in midwater trawls in the Strait of Georgia.

In experiments conducted in 1977/78, 1978/79, and 1979/80, metamorphosed Pacific lamprey in freshwater did not survive past mid-July and most perished by the end of January. In the 1978/79 experiments, salmonids were introduced into the tanks in early February; feeding started in late February to early March and lamprey continued feeding until several weeks prior to death. In 1979/80 experiments, salmonids were introduced into tanks in early October. In three separate experiments, each containing 25–35 lamprey, feeding commenced in mid-October, about the same time as the lamprey from the same rivers commenced feeding in salt water. While the frequency of attacks was lower in freshwater (R. J. Beamish unpublished data), it was apparent that feeding can commence in freshwater and salt water at the same time. The cause of death in these experiments was not determined but if it was related to osmoregulatory problems it may indicate that most stocks of Pacific lamprey must enter salt water soon after metamorphosis is complete and no later than July. Thus the known period of migration into salt water is from December to June and the actual period of migration probably is longer.

Hardisty and Potter (1971) have identified the stage in metamorphosis, after the more obvious external changes have taken place, as the macrophthalmia stage. They consider that in a parasitic species this stage ends with the onset of feeding. Since metamorphosis of Pacific lamprey was complete by mid-October and individuals commenced feeding immediately in freshwater or salt water, it appears that Pacific lamprey metamorphose directly into juvenile adults and the macrophthalmia stage is either very short or it does not exist.

In some locations in British Columbia, lamprey do not migrate into salt water but remain and feed in freshwater (Carl 1953). Mesachie Lake (Fig. 1) contains nonanadromous parasitic lamprey as indicated by the freshly wounded fish that were observed throughout the year. The lamprey captured were immature, feeding, and were larger than most downstream migrants from other rivers. Two lamprey captured in June were acclimated to full strength salt water over a period of 3 d. They were kept in salt water of 6 d indicating that the freshwater residence had not impaired their ability to acclimate to salt water. In subsequent studies these lamprey have been maintained in salt water for several months. Since no physical barrier prevents the adult Pacific lamprey in Mesachie Lake from entering salt water, the term "nonanadromous" rather than "landlocked" more accurately describes their confinement to freshwater. These individuals are morphologically different from other Pacific lamprey and may represent a new species. When recently metamorphosed Pacific lamprey from a number of locations were held in freshwater all Pacific lamprey eventually died except those from Mesachie Lake. While these preliminary experiments show that Mesachie Lake lamprey are different from other Pacific lamprey, it remains unknown if the ability to remain in freshwater is the result of genetic differences or is common to other individuals that traditionally migrate into salt water.

When Pacific lamprey enter salt water they do not remain on or near the surface or in shallow water but move to water deeper than 70 m. Robinson and Barraclough (1968a, b) caught only six Pacific lamprey in surface nets in the vicinity of the Fraser River, and in the present study no Pacific lamprey were found in any surface fishing except in the vicinity of the Fraser River. Pacific lamprey slightly larger than the size of the average downstream migrant have been captured at fishing depths of 100–250 m. Pacific hake (*Merluccius productus*) and walleye pollock (*Theragra chalcogramma*) commonly found at these depths were occasionally found with fresh lamprey wounds. Off the west coast of Vancouver Island during the summer of 1979, salmon fishermen reported small lamprey attached to pink salmon (*Oncorhynchus gorbuscha*) caught a few km to 40 km offshore and at fishing depths of 20–90 m in water of depths to 180 m. By mid-September 1979, nine Pacific lamprey, ranging in size from 16 to 42 cm with an average length of 23 cm had been returned by fishermen and 35 fishermen observed lamprey attached to salmon. The length of the smaller lamprey that were captured was very close to the average size of 17 cm, estimated by these 35 fishermen, and is very similar to the size of Pacific lamprey in their first year of salt water residence in laboratory experiments (R. J. Beamish unpublished data). It appears that the small lamprey found in the Strait of Georgia and off the west coast of Vancouver Island are in their first year of salt water residence and are located at depths in the range of 20 to 250 m.

In laboratory experiments, metamorphosed Pacific lamprey that were maintained in freshwater without food until March, and then acclimated to salt water over a 3-d period, initiated feeding within hours of being introduced into a tank containing Pacific herring. Therefore, it appears that juvenile Pacific lamprey leaving freshwater, move directly into deeper water and probably start feeding immediately.

FEEDING

Rarely are Pacific lamprey observed attached to prey, but the scar or wound that remains on fish frequently has impressions of the teeth, clearly indicating that the wound was caused by a Pacific lamprey. A common prey observed in this study was walleye pollock. Pollock were routinely examined for lamprey attacks from all of the major fishing grounds from 1975 to 1979 and of 21 000 fish examined, 124 fish or about 0.6% were found to have wounds or scars caused by lamprey. The highest incidence of attacks on pollock was observed in Dixon Entrance (54°30′N, 132°39′W), where 10% of a sample of 145 pollock were wounded. More scars or wounds have been observed on the left side of pollock but it is difficult to determine if this apparent preference for the left side is real, as lamprey marks on fish are often observed incidentally to some other project and the degree of sampling bias is unknown at this time. Pacific hake were also examined and of the 50 000 examined 51 or 0.01% were wounded. Pacific hake and walleye pollock are midwater fish that often are found in association with layers of plankton (Beamish et al. 1976) and the attacks on these fish may indicate a preference for this plankton layer by young Pacific lamprey.

Scarring on sockeye salmon by Pacific lamprey in the vicinity of the Fraser River was examined by Williams and Gilhousen (1968) and again in this study. Williams and Gilhousen found that approximately 66% of the sockeye and 20% of the pink salmon sampled had marks of lamprey attacks. Six percent of the wounds on sockeye and 2% of the wounds on pink salmon were considered to be severe. They estimated that mortality due to lamprey wounds after fish moved upstream to the spawning grounds was between 1.6 and 1.8% and was of minor significance. In this study a sample of 681 sockeye from a commercial catch was examined in 1978 for wounds and scars and 27% of the fish were found with evidence of lamprey attacks. Sixty-six percent of the attacks penetrated the skin and 2.4% were severe wounds that penetrated deep into the muscle or body cavity. A sample of 140 sockeye

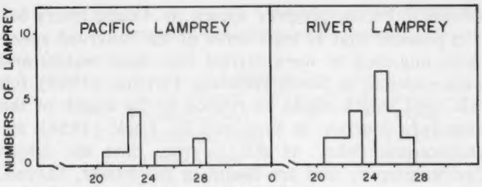

FIG. 8. Length frequency of river lamprey and Pacific lamprey captured in the mouth of the Fraser River Estuary in August–September 1978.

salmon captured during a research cruise, several weeks prior to the examination of the commercial sample contained 17% scarred fish. The higher incidence of scarring in the commercial sample cannot be explained but may be related to the increased time spent in the estuary or may be related to increased attacks on fish that are caught in gill nets. In a combined sample of 821 salmon, 96 attacks were on the right side, 66 were on the left side, 4 were dorsal and 59 were ventral. No explanation for the apparent preference for the right side is possible.

The use of a small mesh purse seine during research cruises in the vicinity of the Fraser River resulted in the capture of Pacific lamprey and river lamprey (Fig. 8) in addition to small and large salmon. On the large sockeye salmon none of the scars in which a tooth pattern could be recognized, appeared to result from river lamprey attacks but many of the smaller salmon had been attacked by river lamprey.

Mason (1974) observed that 61 of 539 coho salmon (14%) returning to Lymn Creek in 1971 had lamprey scars and 137 of 348 in 1972 (45%) had scars. Female coho had significantly more scars than males. Six of 30 sockeye salmon returning to Sproat Lake and 10 of 68 sockeye salmon returning to Great Central Lake had evidence of lamprey attacks. Six fish from the two samples suffered more than one attack and four of the fish had suffered attacks that did not penetrate the skin. Most wounds did penetrate the skin and were approximately 5 mm in diameter, indicating attacks by small, young lamprey. No lamprey were observed on any of the 60 000 sockeye salmon that were counted entering these lakes. Birman (1950) also noted a high percentage (44%) of scars caused by Pacific lamprey on pink salmon in the Amur estuary.

Because the sockeye salmon were returning to spawn and some of the attacks had not penetrated the skin it might appear that the lamprey were also aggregating in preparation to return to freshwater. Soldatov (1934) considered that lampreys gathered in estuaries of larger rivers and attached to salmon that were moving upstream in order to accelerate their own movement into freshwater. However, two of nine Pacific lamprey that were collected in the Fraser River estuary in August in 1976 and measured 20 and 23 cm, were alive in the laboratory in August 1979. The presence of young lamprey in these aggregations, the failure to observe lamprey attached to migrating maturing salmon in freshwater and the observation that maturing Pacific lamprey enter freshwater in the spring, indicates that the aggregations of Pacific lamprey contain younger lamprey and not adults preparing to migrate immediately into freshwater unlike the river lamprey that were captured at the same time.

Pacific lamprey in this study were observed to attack rockfish (*S. aleutianus* and *S. reedi*), Pacific cod (*Gadus macrocephalus*), chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*), lingcod (*Ophiodon elongatus*), and sable fish (*Anoplopoma fimbria*). Pike (1950, 1951) recorded lamprey attacks on steelhead trout (*Salmo gairdneri*), Pacific halibut (*Hippoglossus stenolepis*), and whales. In the Bering Sea Pacific lamprey fed on the greenland turbot (*Reinhardtius hippoglossoides*), the arrowtooth flounder (*Atheresthes stomias*), the Kamchatka flounder (*Atheresthes evermanni*), sablefish, Pacific ocean perch (*Sebastes alutus*), and Pacific cod (Novikov 1963; Abakumov 1964). In one study in the Bering Sea, Pacific lamprey attacks were observed on about one-third of all greenland turbot examined (Novikov 1963) and as many as 55% in some hauls had scars or fresh lamprey wounds (Abakumov 1964). The lamprey attacks were almost exclusively on the blind side.

Unlike river lamprey, Pacific lamprey feed in a manner similar to the sea lamprey (Parker and Lennon 1956). Pacific lamprey attacked ventrally and anteriorly leaving 1–3 cm holes in the flesh. A common place of attachment on pollock was just behind the pectoral fin. The anterior ventral area was a common scarring location on sockeye salmon. In the laboratory and in the ocean, multiple attachments occur especially by young metamorphosed lamprey. In the laboratory, lamprey will remain attached to a host for varying periods that last up to several days. Feeding in the laboratory continued throughout the year suggesting feeding in the ocean continues throughout the year.

DISTRIBUTION

From 1975 to mid-1979, 66 Pacific lamprey were captured during fishing operations on research cruises in the Strait of Georgia. In addition, fishermen frequently captured Pacific lamprey attached to sockeye salmon caught in troll and gill nets in the Strait of Georgia. For example, on August 26 to 27, 1979 one fisherman landed 17 Pacific lamprey that ranged in size from 16 to 20 cm. Only nine Pacific lamprey have been obtained from other areas off British Columbia; however, scars or wounds have been observed during research cruises off the west coast of the Queen Charlotte Islands, in Dixon Entrance, Hecate Strait, Queen Charlotte Sound, and off the west coast of Vancouver Island. The relatively large number of lamprey attacks reported in the area off the west coast of Vancouver Island may indicate a relatively high abundance in this area. It is expected that other areas of high relative abundance will be identified in the future because observations of lamprey attacks and collections of lamprey have been solicited from fishermen only in the last few years. Despite the relatively few accounts of lamprey attacks, Pacific lamprey have been observed in all the important commercial fishing areas off Canada's west coast and their number and distribution certainly are greater and more widespread than indicated by current reports.

PREDATION ON PACIFIC LAMPREY

The extent that other animals feed on Pacific lamprey is unknown but various accounts of animals feeding on lamprey indicate that lamprey may be consumed more often than formerly thought. Eighty-two percent of the observed feedings of Steller sea lions (*Eumetopias jubatus*) feeding at the mouth of the Klamath River, California were on Pacific lamprey. Two sea lions that were shot had stomach contents composed entirely of Pacific lamprey (Jameson and Kenyon 1977). One of a group of seals thought to be feeding on sockeye salmon smolts in the Skeena River was shot as part of a program to reduce the nuisance to salmon net fishermen (the program was terminated about 1962). The stomach of the seal contained two lamprey apparently from a group of nearby spawning lamprey (A. Peden, British Columbia, Provincial Museum, personal communication). A fishery officer in the Skeena River area reported that in January he observed a mink (*Mustela vison*) with a live lamprey in its mouth. Pacific lamprey have also been found in the stomach of a sperm whale (*Physeter catodon*) (Pike 1950) and fur seals (Hubbs 1967). In the present study, portions of tails of upstream migrating adult lamprey in freshwater occasionally were missing. In a laboratory experiment, a spiny dogfish (*Squalus scanthias*) bit off the posterior 2–3 cm of the tail of a lamprey and the lamprey survived. As part of another study, spiny dogfish and sablefish fed actively on freshly killed adult Pacific lamprey, consuming about two to three lamprey each in a 15-min period.

MOVEMENTS AND DURATION OF SALTWATER LIFE

Little evidence is available to indicate whether or not Pacific lamprey from Canadian rivers migrate extensive distances. Larkins (1964) recorded catches of Pacific lamprey during a high seas salmon sampling program suggesting that Pacific lamprey do actually move into the high seas. However, the catches were made 60–150 km south of the Aleutian Islands and possibly were fish from local rivers on the Aleutian Islands. Pacific lamprey have been observed in the central and western regions of the Bering Sea (Novikov 1963) and in rivers in Japan (Hubbs 1971). It is unknown if Pacific lamprey spawn in Asiatic rivers but it is possible that at least some of the observed specimens migrated or were carried into these waters and were endemic to North America. Pletcher (1963) felt that total length might be related to the length of the migratory journey as proposed by Lack (1954) for anadromous fishes. If this is true, then the larger Pacific lamprey that are found in the Fraser, Skeena, and Stamp rivers (40–72 cm range) may range farther than some stocks of smaller Pacific lamprey. It is also possible that size may be related to the duration of feeding, and that lamprey spending longer periods in salt water grow to larger sizes. Certainly Pacific lamprey move offshore and it is probable that some lamprey or some stocks of lamprey migrate considerable distances.

The length of time spent by Pacific lamprey in salt water is unknown and possibly is different for different stocks. Since traditional methods of age determination or tagging could not be used to estimate the time spent in salt water, a simple laboratory holding and feeding experiment was initiated in October 1975 using 15 Pacific lamprey that were captured during midwater trawling operations in June 1975 in the Strait of Georgia (Fig. 7). These lamprey ranged in length from 18 to 40 cm and in weight from 13 to 83 g. They were given salmon and a variety of other species to feed on and were left untouched. By December 1975, 12 lamprey remained alive; in December 1976, 7 remained; in December 1977, 4 remained and in December 1978, 3 were alive. One died and one was lost in January 1979 and the remaining fish died in May 1979. Some lamprey died as a result of culture problems, but most dead fish were mature and presumably ready to spawn. If December can be considered to approximate the time of entry into salt water, the three lamprey alive in December 1978 completed at least 4-yr residence in salt water. Similar experiments were repeated in 1976, 1977, 1978, and 1979 and the results to date are similar.

It is possible that the remaining fish in December 1978 were older than one year in December 1975 and it also can be argued that if these lamprey had been in a natural system they would return to freshwater at an earlier date. River lamprey held in tanks in this study did not survive past the normal spawning time indicating laboratory observations were representative of the natural life cycle. Most landlocked sea lamprey (*Petromyzon marinus*) held in laboratory tanks, matured and showed signs of irreversible physical degeneration (Parker and Lennon 1956) at about the same time as reported for wild fish (Applegate 1950). However, Parker and Lennon (1956) did observe that a few lamprey survived longer than others. Thus it appears that holding in the laboratory may extend the parasitic life of some lamprey. It is also possible that some lamprey do have a longer parasitic period than other individuals of the same species since variation in the duration of saltwater life is known to occur

TABLE 5. Size of maturing Pacific lamprey in freshwater.

Location		Mean length (cm)	Range (cm)	No.
Quinsam River	1978[a,h]	20	18–26	7
Chemainus River	1978[b,h]	27	17–38	131
Bonsall Creek	1978[b,h]	26	13–31	18
Qualicum River	1978[a,h]	19	16–24	6
Kennedy Lake tributary river	1979[a,c,h]	29	23–45	5
Robertson Creek	1978[a,d,j]	28	22–40	11
Babine Lake unnamed creek	1979[a,e,j]	49	42–59	52
	1979[i]	48	41–56	255
	total	48	41–59	307
Babine Lake	1979[b,e,i]	64	55–67	14
Bulkley Falls	1979[b,f,j]	60	55–69	32
	1979[i]	58	48–65	46
	total	59	48–69	78
Moricetown Falls	1979[b,g,i]	64	56–72	9
Stamp River	1979[b,j]	29	23–51	1226

[a] Sampled during spawning period.
[b] Sampled during upstream migration.
[c] 49°35′N, 125°30′W.
[d] Robertson Creek is located in the vicinity of Stamp River (Fig. 1).
[e] 54°N, 126°W.
[f] 54°29′N, 129°16′W.
[g] 55°02′N, 127°41′W.
[h] Measured after preservation in 5% formalin.
[i] Measured after freezing.
[j] Measured with no preservation.

for other anadromous fishes such as sockeye and chinook salmon (Hart 1973). If the laboratory observations are representative of a natural life cycle, Pacific lamprey remain and feed in salt water for a period up to 3½ yr if they return to freshwater in the spring.

There is a wide range in the size of adult Pacific lamprey. This difference in size is most obvious when the sizes of returning adults are examined (Table 5). The sizes recorded in freshwater probably underestimate the maximum size because maturing adult lamprey decrease in length as observed in this study and for other species (Beamish 1980; Larsen 1973). While the sample size in Table 5 is small it is apparent that mature Pacific lamprey range in length from 13 to at least 72 cm. Pletcher (1963) also describes a wide range of lengths for Pacific lamprey. The 66 specimens captured in this study in the Strait of Georgia and the 9 specimens found in other areas off the west coast of Canada ranged in size from 12 to 42 cm. It is possible that the very small mature Pacific lamprey found in the Qualicum and Quinsam rivers may not remain in salt water as long as the larger lamprey and some may even remain in freshwater. Until more information is available it might be assumed that the moderate to large lamprey (25–50 cm) spend approximately 3½ yr in salt water.

SEX RATIO

Little information was available concerning the sex ratio of adults captured at sea. Thirty-nine of the 61 specimens captured in the Strait of Georgia were sexed and the ratio was 1.4 males to 1 female. The sex ratios of males to females returning to the Stamp River, Bulkley River, Babine Lake, Chemainus River and Bonsall Creek were 2:1, 0.8:1, 1:1, 1:1, 1:1, respectively. Except for the Stamp River sample, the ratio of males to females was equal, thus it is probable that sex ratios at sea are about equal.

RETURN TO FRESHWATER

Since larger Pacific lamprey are found in only some rivers such as in the Skeena River system, it is probable that at least some lamprey return to their native streams to spawn. However, more information about the size compositions of adults from more rivers is needed before the importance of homing can be assessed.

Pacific lamprey have been reported to return to freshwater from May to September, overwinter in freshwater and spawn April to June and possibly as late as July (Pletcher 1963, Carl et al. 1967, Moffett and Smith 1950). In the Chemainus River, except for a few days, upstream traps were in place close to the mouth of the river from April 20 until June 27. A total of 131 adult lamprey were captured during the period April 23 to May 31 with 94% of the catches occurring between May 5 and 10. Sixty males and 64 females were captured with about equal numbers of males and females in the daily catches. In Bonsall Creek, the upstream trap close to the mouth of the river captured 18 adult Pacific lamprey from May 1 until May 17. The trap was in operation from April 15 until June 1 and equal numbers of males and females were captured.

In the Stamp River, Pacific lamprey were collected in an artifical river bypass or fishway, 14 km from the mouth of the river. The first sample was collected in mid-June, 1979 from an estimated 2500 individuals and at the end of August approximately 300 lamprey were still migrating through the fishway. Observations of movements of tagged lamprey confirmed that the lamprey were actually migrating through the fishway. By the end of September the fishway contained about 250 lamprey. While some lamprey tagged in August were still migrating through the fishway in September it appeared that most lamprey had completed their migration by mid-August. In 1980 no migration was observed until May and since the fishway is approximately 14 km from the ocean it is probable that upstream migrations commenced in April. At a fish counting fence, 400 km from the mouth of the Skeena River and 13 km downstream from Babine Lake, upstream migrating Pacific lamprey were first observed in mid-August at about the same time Pacific lamprey were observed in other tributaries of the Skeena River (Table 5). It was interesting that Pacific lamprey were observed spawning in the Babine Lake area in early July 1979 only 4–6 wk prior to the arrival of next year's spawning individuals. Since these sites are approximately 400 km from the mouth of the Skeena River it is probable that entry into freshwater occurred in April-May as observed in other rivers. Migration into one of the smaller headwater streams of the Skeena River was completed by the end of September 1979. The lamprey apparently remain in the uppermost region of the stream or in a small lake until they spawn in mid-June. Richards (1980) observed young-of-the-year ammocoetes in the uppermost regions of the tributary streams of the Chemainus River indicating adults migrated well upstream prior to spawning. The movement of adult Pacific lamprey into the headwater areas, often through rapids and over waterfalls indicates the species has exceptional migratory instincts. Spawning in the uppermost areas also allows for maximum usage of suitable stream habitats assuming young ammocoetes gradually migrate downstream.

Ovaries from upstream migrating lamprey in the Stamp River in August and the Skeena River in September occupied less than one-third to about two-thirds of the body cavity, respectively. Egg diameters for lamprey from the Stamp and Skeena rivers were approximately 1.0 and 0.7 mm, respectively. The abdomens of all females were not distended and there was no evidence of postanal length reductions or dorsal fin space reductions. Although the females were maturing there was little doubt that they were not close to spawning condition, indicating spawning would not occur until the following spring. Upstream migrants from the Stamp River, held in the laboratory in 1979/80, did not spawn until the spring following entry into freshwater.

It is important that a distinction is made between the time upstream migrations occur in freshwater and the time Pacific lamprey enter freshwater. The observations in this study indicate that entry into freshwater occurs from April to June while most migrations in freshwater streams probably are complete by late September. The statement that the return to freshwater occurs from May to October (Moffett and Smith 1950; Pletcher 1963; Hart 1973) fails to acknowledge that most lamprey enter freshwater early in the spring. This can result in the incorrect assumption mentioned earlier, that Pacific lamprey feeding on maturing salmon in estuaries migrate upstream with the salmon.

Spawning lamprey in June and July in Babine Lake averaged 48 cm in length (Table 5). Lamprey returning to Babine Lake, Bulkley Falls, and Moricetown Falls in August and September, all migrate up the Skeena River and had a similar mean length of 60 cm (Table 5). If average lengths are similar each year, Pacific lamprey in the Skeena River system decrease approximately 12 cm in length from the postmigration period until spawning is complete. This 20% average decrease in length is similar to the 21% decrease previously described for river lamprey, but undoubtedly underestimates the actual amount of shrinkage since the lengths at the time of entry into freshwater were unknown. As reported for other species (Beamish 1980) there was a disproportionate reduction in length of females (23%) compared to males (15%).

Pletcher (1963) observed that April to May was the main spawning period for Pacific lamprey. In this study, Pacific lamprey were observed spawning in a small stream flowing into Babine Lake in early July, 1979 and Pacific lamprey have been observed spawning in the Stamp River in April and in the Englishman River (Fig. 1) in June. Since entry into freshwater occurs from April to June and spawning occurs from April until early July, the average residence of maturing adults in freshwater is about 1 yr. If the period of saltwater residence is about 3½ yr for adults returning to freshwater in the spring, then the period of adult life from the onset of metamorphosis in July to death following spawning is 5 yr.

In smaller rivers, smaller Pacific lamprey were observed to spawn several kilometres from the mouth of the river. It is possible that entry into such rivers occurs in the same year as spawning and the length of saltwater residence may be shorter or longer than 3½ yr.

The spawning and nesting behavior of the Pacific lamprey has been described by Pletcher (1963) and appears to be similar to that of other lamprey. Following spawning, Pacific lamprey have been reported to survive until July (Moffett and Smith 1950). In this study dead, spawned Pacific lamprey were observed in Robertson Creek on Vancouver Island in late April and in Babine Lake in July. A sample of eight live

Pacific lamprey of various sizes that had recently spawned, died when they were reintroduced to full strength salt water in the laboratory over a 3-d period. A sample of six upstream migrating adult lamprey, collected in August 1979 from the fishway at Stamp River also could not be acclimated to salt water over a 3-d period. Thus, after Pacific lamprey enter freshwater in preparation for spawning, they do not return to salt water.

EFFECT ON COMMERCIALLY IMPORTANT FISHES IN WATERS OFF CANADA'S WEST COAST

Very little is known about the size of stocks of Pacific lamprey, however, casual observations at fish counting fences and by commercial fishermen indicate that the numbers of Pacific lamprey may be increasing, at least in some areas. No Pacific lamprey were observed at the fish counting fence near Babine Lake from 1956 to 1962. From 1963 to the present the number of lamprey at the fence has been increasing (F. Jordan, Pacific Biological Station, Nanaimo, B.C., personal communication) and in 1977 I received the first unconfirmed report of a lamprey attacking a fish in Babine Lake. Williams and Gilhousen (1968) reported that fishermen first reported cases of severe lamprey parasitism on Fraser River sockeye in 1967. In 1979 several fishermen reported their first observations of lamprey attacking salmon off the west coast of Vancouver Island, while others reported the incidence of lamprey attacks on salmon was higher than in the past.

The number of streams and rivers that contain Pacific lamprey is unknown. However, Carl et al. (1967) believed Pacific lamprey may be present in all coastal streams and in this study all of the 10–20 streams that have been examined have contained Pacific lamprey. If all or almost all of the coastal streams and rivers contain Pacific lamprey, the numbers of adults may be large, and if Pacific lamprey remain in salt water for 3½ yr they may be an important and overlooked predator of juvenile and adult marine fishes.

Pacific lamprey contribute to the mortality of young salmon but the relative importance of this mortality is unknown. Active predation on juvenile sockeye salmon was observed in this study in the Strait of Georgia and some preliminary unpublished trapping information indicates that in some rivers the movements of Pacific lamprey and juvenile sockeye salmon into salt water are synchronous. Preliminary results from laboratory feeding experiments indicate that one Pacific lamprey in its first year in salt water can kill one salmon of 15–20 cm in length about every 2–4 d. Thus the attacks and in some cases resulting mortalities may be more important than formerly thought. The nonanadromous parasitic lamprey in Mesachie Lake attack a significant number of the resident salmonids. A sample of 221 salmonids contained 122 fish with lamprey attacks and 32 of these attacks (15%) penetrated the body cavity or penetrated deeply into the muscle and probably would result in the death of the fish. Salmonids that were killed by lamprey attacks have been found on the bottom of Mesachie Lake from June until September when observations were terminated. It is apparent that Pacific lamprey are an active predator of marine and sometimes freshwater fishes; however, their role as a predator of commercially important species in relation to other predators is difficult to assess until better estimates of their abundance and food preferences can be determined.

Comparisons and Conclusions

While there is much more to learn about river and Pacific lampreys, it is apparent that the two species differ greatly in many aspects of their adult biology. It is suspected that the date of metamorphosis is similar but it appears that Pacific lamprey enter salt water earlier and perhaps over a longer period. Downstream trapping and fishing in salt water suggested that Pacific lamprey enter salt water in late fall or early winter and continue to enter salt water into the summer. The bulk of river lamprey catches occurred in downstream traps in late May and June and no river lamprey were found in salt water in April or May.

Once in salt water, river lamprey were found in the surface waters and concentrated in the general vicinity of the larger rivers suggesting river lamprey preferred water of reduced salinity. Pacific lamprey were found at greater depths often associated with layers of plankton. Pacific lamprey were more abundant than river lamprey but river lamprey could not be considered to be rare. While Pacific lamprey or evidence of Pacific lamprey attacks were observed on fishes associated with the midwater depths, the evidence of rather substantial predations on greenland turbot from the Bering Sea indicates that this species occurs throughout a wide depth range when at sea. Pacific lamprey or animals attacked by Pacific lamprey were caught well offshore indicating that Pacific lamprey migrated greater distances than river lamprey. River lamprey had a more restrictive diet preferring smaller herring and some smaller salmon. They attacked dorsally and anteriorly and consumed chunks of tissue. Pacific lamprey may feed on herring when first in salt water but generally feed on a variety of fishes and mammals. Pacific lamprey attacked ventrally or laterally apparently preferring body fluids to chunks of flesh.

Adult Pacific lamprey can be much larger than river lamprey, partly as a result of the longer period Pacific lamprey spend in salt water. Pacific lamprey can remain in salt water for 3½ yr while river lamprey may spend only 3–4 mo in salt water. River lamprey may return to freshwater over the period September to May but stocks of Pacific lamprey enter freshwater from April to June. The period of freshwater residence for most maturing Pacific lamprey is about 1 yr but it may be shorter for some other stocks. The period of freshwater residence for maturing river lamprey may be about 8 mo or shorter. Both species decrease in length during the prespawning residence in freshwater and in this study both species decreased in length by approximately 20%. Both species die following spawning.

Predators on adult river lamprey appear rare while Pacific lamprey may be a more common food item of fishes, seals, sea lions, and mammals. It is possible that ammocoetes of both species are consumed by other fishes.

Lampetra ayresi was considered to be conspecific with the European river lamprey *Lampetra fluviatilis* before Vladykov and Follett (1958) reviewed the systematics of those two forms and concluded that they were separate species. Even though these two forms are now considered to be distinct species there are some remarkable similarities in their adult biology. *Lampetra fluviatilis* may prefer water of reduced salinity (Bahr 1952) and feeds on small fish apparently preferring herring species (Bahr 1933; Eglite 1958a, b). When feeding, chunks of muscle, pieces of fins, and internal organs are consumed and attacks frequently occur in the dorsal region (Eglite 1958a). Adults returning to freshwater average 31–34 cm (Berg 1948) but a wide range in sizes of adults has been found. The smaller forms have been described by Berg (1948) as being distinct "praecox" varieties. Berg (1948) noted that some adults return to freshwater in the fall and some in the spring. Hardisty and Potter (1971) consider that from metamorphosis to spawning the duration of adult life of *Lampetra fluviatilis* is about 2½ yr. This is slightly longer than the period of 2 yr observed for *Lampetra ayresi* in this study.

All of the preceding adult characteristics of *Lampetra fluviatilis* were similar to *Lampetra ayresi*. The similarities in form and the biology of the adults of these two species clearly suggest a close relationship at some time in the past.

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ABAKUMOV, V. A. 1964. Some data on the ocean period in the life-cycle of lamprey (*Entosphenus tridentatus* Richardson). Trudy vses. nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 49: 253–256. (In Russian)

APPLEGATE, V. C. 1950. Natural history of the sea lamprey, *Petromyzon marinus* in Michigan. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. 55: 237 p.

BAHR, K. 1933. Das Flussneunauge (*Lampetra fluviatilis*) als Urheber von Fischverletzungen. Mitt. Dtsch. Seefisch. Ver. 49(1): 3–8.

1952. Beitraege zur Biologie des Flussneunauges, *Petromyzon fluviatilis* L. (Lebensraum und Ernaehrung). Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere. 81: 408–436.

BARRACLOUGH, W. E., AND J. D. FULTON. 1967. Data record. Number, size composition and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia July 4–8, 1966. Fish. Res. Board Can. MS Rep. 940: 82 p.

BEAMISH, F. W. H. 1980. Biology of the North American anadromous sea lamprey, *Petromyzon marinus*. Can. J. Fish. Aquat. Sci. 37: 1924–1943.

BEAMISH, R. J., AND J. R. SCARSBROOK. 1979. Data for the study of the distribution and feeding habits of lampreys in the surface waters of the Gulf Islands and in the vicinity of the Fraser River, British Columbia. Fish. Mar. Serv. Data Rep. 136: 353 p.

BEAMISH, R. J., M. SMITH, R. SCARSBROOK, AND C. WOOD. 1976. Hake and pollock study, Strait of Georgia cruise G. B. REED, June 16–27, 1975. Fish. Mar. Serv. Data Rec. 1: 174 p.

BEAMISH, R. J., AND N. E. WILLIAMS. 1976. A preliminary report on the effects of river lamprey (*Lampetra ayersii*) predation on salmon and herring stocks. Fish. Mar. Serv. Res. Dev. Tech. Rep. 611: 26 p.

BERG, L. S. 1948. Freshwater fishes of the USSR and adjacent countries. Acad. Sci. USSR. Zool. Inst.: Guide to the Fauna of the USSR, No. 27. (Transl. from Russian for Nat. Sci. Found., Wash., D.C. by the Israel Program for Scientific Translations, Jerusalem, 1962. Vol. 1: 18–52, 494.)

BIRMAN, I. B. 1950. Parasitism of salmon of the genus *Oncorhynchus* by the Pacific lamprey. Vladivostok. Tikhookean. Nauchno-issled. Inst. Rybn. Khoz. Okeanogr. (TINRO) Izv. 32: 158–160. (Transl. from Russian by Fish. Res. Board. Can., Transl. Ser. 290 (1960): 3 p.)

CARL, G. C. 1953. Limnobiology of Cowichan Lake, British Columbia. J. Fish. Res. Board Can. 9: 417–449.

CARL, G. C., W. A. CLEMENS, AND C. C. LINDSEY. 1967. The freshwater fishes of British Columbia. B.C. Prov. Mus., Handbook No. 5: 192 p.

EGLITE, R. 1958a. Feeding habits of *Lampetra fluviatilis* L. in the sea. Zool. Zh. 37(10): 1509–1514.

1958b. The biology of the river lamprey in the Latvian SSR. Gidrobiol. Issled., Tartu 1: 234–269.

HANSON, L. H., E. L. KING JR., J. H. HOWELL, AND A. J. SMITH. 1974. A culture method for sea lamprey larvae. Prog. Fish-Cult. 36(3): 122–128.

HARDISTY, M. W., AND I. C. POTTER [ed.]. 1971. The biology of lampreys. Academic Press. London, New York. Vol. 1: 424 p.

HART, J. L. 1973. Pacific fishes of Canada. Bull. Fish. Res. Board Can. 180: 740 p.

HUBBS, C. L. 1967. Occurrence of the Pacific lamprey, *Entosphenus tridentatus*, off Baja California and in streams of Southern California; with remarks on its nomenclature. Trans. San Diego Soc. Nat. Hist. 14: 301–312.

1971. *Lampetra* (*Entosphenus*) *lethophaga*, new species, the nonparasitic derivative of the Pacific lamprey. Trans. San Diego. Soc. Nat. Hist. 16: 125–164.

JAMESON, R. J., AND K. W. KENYON. 1977. Prey of sea lions in the Rogue River, Oregon. J. Mammal. 58(4): 672.

KAN, T. T. 1975. Systematics, variation, distribution and biology of lampreys of the genus *Lampetra* in Oregon. Ph.D. thesis, Oregon State Univ., Corvallis, OR. 194 p.

LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford. 343 p.

LARKINS, H. A. 1964. Some epipelagic fishes of the North Pacific Ocean, Bering Sea, and Gulf of Alaska. Trans. Am. Fish. Soc. 93: 286–290.

LARSEN, L. O. 1973. Development in adult, freshwater river lampreys and its hormonal control. Starvation, sexual maturation and natural death. Copenhagen. 172 p.

MASON, J. C. 1974. Movements of fish populations in Lymn Creek Vancouver Island: a summary from weir operations during 1971 and 1972 including comments on species life histories. Fish. Mar. Serv. Tech. Rep. 483: 35 p.

MOFFETT, J. W., AND S. H. SMITH. 1950. Biological investigations of the fishery resources of Trinity River, California. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. 12: 70 p.

MORRIS, R. 1971. Osmoregulation, p. 193–239. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2. Academic Press, London and New York.

NOVIKOV, N. P. 1963. Attacks of *Entosphenus tridentatus* on halibut and other fish of the Bering Sea. Vopr. Ikhtiol. 3(28): 567–569.

PARKER, P. S., AND R. E. LENNON. 1956. Biology of the sea lamprey in its parasitic phase. U.S. Fish. Wildl. Serv. Res. Rep. 44: 32 p.

PIKE, G. C. 1950. Stomach contents of whales caught off the coast of British Columbia. Fish. Res. Board Can. Prog. Rep. Pac. Coast Stations 83: 27–28.

1951. Lamprey marks on whales. J. Fish. Res. Board Can. 8(4): 275–280.

PLETCHER, F. T. 1963. The life history and distribution of lampreys in the Salmon and certain other rivers in British Columbia, Canada. MSc. thesis, Univ. British Columbia, Vancouver, B.C. 195 p.

RICHARDS, J. E. 1980. Freshwater life history of the anadromous Pacific lamprey *Lampetra tridentata*. M.Sc. thesis, Univ. Guelph, Guelph, Ont., Canada. 99 p.

ROBINSON, D. G. 1969. Data record. Number, size composition, weight and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia July 4–6, 1967. Fish. Res. Board Can. MS Rep. 1012: 71 p.

ROBINSON, D. G., W. E. BARRACLOUGH, AND J. D. FULTON. 1968a. Data record. Number, size composition, weight and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia May 1–4, 1967. Fish. Res. Board Can. MS Rep. 964: 105 p.

1968b. Data record. Number, size composition, weight and food of larval and juvenile fish caught with a two-boat surface trawl in the Strait of Georgia June 5–9, 1967. Fish. Res. Board Can. MS Rep. 972: 109 p.

ROOS, J. F., P. GILHOUSEN, S. R. KILLICK, AND E. R. ZYBLUT. 1973. Parasitism on juvenile Pacific salmon (*Oncorhynchus*) and Pacific herring (*Clupea harengus pallasi*) in the Strait of Georgia by the river lamprey (*Lampetra ayresi*). J. Fish. Res. Board Can. 30: 565–568.

SCARSBROOK, J. R., R. J. BEAMISH, AND M. S. SMITH. 1980. Hake and pollock study, Strait of Georgia, G. B. REED cruise May 31–June 18, 1976. Can. Data. Rep. Fish. Aquat. Sci. (In press)

SOLDATOV, V. K. 1934. Fishery Ichthyology. Part I. Cited by I. B. Birman. 1950. Fish. Res. Board Can., Transl. Ser. 290: 3 p.

VLADYKOV, V. D., AND W. I. FOLLETT. 1958. Redescription of *Lampetra ayresii* (Günther) of western North America, a species of lamprey (Petromyzontidae) distinct from *Lampetra fluviatilis* (Linnaeus) of Europe. J. Fish. Res. Board Can. 15(1): 47–77.

1965. *Lampetra richardsoni*, a new nonparasitic species of lamprey (Petromyzonidae) from western North America. J. Fish. Res. Board Can. 22: 139–158.

WALDICHUK, M. 1957. Physical oceanography of the Strait of Georgia, British Columbia. J. Fish. Res. Board Can. 14: 321–486.

WILLIAMS, I. V., AND P. GILHOUSEN. 1968. Lamprey parasitism on Fraser River sockeye and pink salmon during 1967. Int. Pac. Salmon. Fish. Comm. Prog. Rep. 18: 22 p.

WITHLER, F. C. 1955. Coho salmon fingerling attacked by young lamprey. Fish. Res. Board Can. Pac. Prog. Rep. 104: p. 15.

YOUSON, J. H., AND I. C. POTTER. 1979. A description of the stages in the metamorphosis of the anadromous sea lamprey, *Petromyzon marinus* L. Can. J. Zool. 57: 1808–1817.

Biology of the North American Anadromous Sea Lamprey, *Petromyzon marinus*[1]

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Beamish, F. W. H. 1980. Biology of the North American anadromous sea lamprey, *Petromyzon marinus*. Can. J. Fish. Aquat. Sci. 37: 1924–1943.

The sea lamprey (*Petromyzon marinus*) in the western Atlantic Ocean adjacent to North America is usually found within a depth of 200 m between latitudes of 30 and 53°. Spawning size lampreys have been recorded in 116 rivers between 32 and 48° latitude. The upstream spawning migration which may extend to several hundred kilometres, takes place between March and September, the actual time varying directly with latitude. Fecundity of the anadromous *P. marinus* (approximately 124 000–305 000) is the highest for any lamprey species. Energy requirements for migration and reproduction are discussed in the context of parental investment. The larval phase lasts 6–8 yr and is followed by a highly synchronous period of metamorphosis. On completion of metamorphosis in late autumn some juveniles migrate downstream to the estuary or ocean and commence feeding. In at least some rivers, a portion of the young juveniles overwinter in the natal stream without feeding. Subsequent to a short feeding period in May these young juveniles leave the river for the sea. Sea lampreys attack a variety of marine elasmobranchs and teleosts. Only swordfish, *Xiphias gladius*, and striped bass, *Roccus saxatilis*, are reported to eat lampreys. During the marine interval, which lasts from 23 to 28 mo, the calculated instantaneous growth rate is 0.645–0.785 $g \cdot d^{-1}$. Lamprey scarring frequency on Atlantic salmon, *Salmo salar*, in the St. John River, New Brunswick, increased from 2.6 to 15.0% between 1972 and 1975 coincident with a dramatic rise in the number of migrant salmonids. Scars were most prevalent on larger salmon, particularly females. Most scars were recorded on the right side of salmon, particularly in the ventral regions.

Key words: sea lamprey, Atlantic Ocean, distribution, life cycle, growth, energetics, fecundity

Beamish, F. W. H. 1980. Biology of the North American anadromous sea lamprey, *Petromyzon marinus*. Can. J. Fish. Aquat. Sci. 37: 1924–1943.

La grande lamproie marine (*Petromyzon marinus*) de l'océan Atlantique occidental adjacent à la côte nord-américaine se rencontre ordinairement en dedans de 200 m de profondeur entre les latitudes 30 et 53°. On a signalé des lamproies de taille à se reproduire dans 116 rivières situées entre 32 et 48° de latitude. La migration de ponte vers l'amont, qui peut couvrir plusieurs centaines de kilomètres, a lieu entre mars et septembre, le moment précis variant en fonction directe de la latitude. Parmi les espèces de lamproies, *P. marinus* anadrome est l'espèce la plus féconde (produisant approximativement 124 000 à 305 000 oeufs). Les besoins énergétiques pour la migration et la reproduction sont analysés dans le contexte de l'investissement parental. La phase larvaire dure de 6 à 8 ans, et elle est suivie d'une métamorphose très étroitement synchronisée. Une fois celle-ci terminée fin automne, quelques jeunes descendent vers l'estuaire ou l'océan et commencent à se nourrir. Dans quelques rivières au moins, un certain nombre de jeunes lamproies passent l'hiver dans le cours d'eau natal sans se nourrir. Après une courte période d'alimentation en mai, ces jeunes quittent la rivière et se dirigent vers la mer. La grande lamproie marine attaque un variété d'élasmobranches et de téléostéens marins. L'espadon, *Xiphias gladius*, et le bar d'Amérique, *Roccus saxatilis*, sont les seuls poissons qui ont la réputation de manger des lamproies. Durant la période en mer, qui dure de 23 à 28 mois, le taux de croissance instantané calculé est de 0,645 à 0,785 $g \cdot d^{-1}$. La fréquence des cicatrices de lamproies sur le saumon atlantique, *Salmo salar*, dans la rivière Saint-Jean, au Nouveau-Brunswick, passa de 2,6 à 15,0% entre 1972 et 1975, en même temps qu'une augmentation spectaculaire du nombre des salmonidés migrateurs. Les cicatrices étaient plus fréquentes chez les grands salmonidés, en particulier les femelles. La plupart des cicatrices se trouvent sur le côté droit du saumon, surtout dans la région ventrale.

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THE anadromous sea lamprey is widely distributed within the Atlantic drainages of North America from the coast of Labrador, as far south as Florida, and throughout eastern Europe from Varanger Fjord in Norway to the western Mediterranean (Bigelow and Schroeder 1948; Hubbs and Potter 1971). This paper presents a synthesis of the published and new information on the biology of the anadromous sea lamprey from eastern North America.

The anadromous sea lamprey reproduces in many but not all North American tributaries to the western Atlantic (Bigelow and Schroeder 1948). The larval stage is spent largely in burrows within the sandy silt substrate of the natal stream. The duration of larval life is difficult to determine because of the variability in ammocoete growth rate as well as the absence of bone. Beamish and Potter (1975) estimated that the larval period is 6–8 yr. Following a nontrophic period of metamorphosis (Ooi and Youson 1977; Youson et al. 1977; Potter et al. 1978) some of the young juveniles migrate downstream in late autumn to the estuary or coastal marine environment and commence feeding on fish (Mansueti 1962). Others remain in the river over winter without feeding (Beamish and Potter 1975; Potter and Beamish 1977). In early spring these young juveniles migrate downstream following a short but essential period of active feeding (Beamish et al. 1978). The duration of the juvenile feeding phase is unknown but is thought to last for 2 or even 3 yr (Potter and Beamish 1977). Thereafter anadromous sea lampreys leave the ocean and complete their life cycle on spawning nests constructed in the gravel substrate of rivers.

Materials and Methods

Ammocoetes and metamorphosing sea lampreys were collected by electro-shocker in New Brunswick from the Nashwaaksis River, a tributary of the St. John River, from the northwest branch of the Miramichi and from the Petitcodiac River (Beamish and Potter 1975; Fig. 1). After anesthetization in methane tricaine sulfonate (Sandoz), the length of each animal was measured to the nearest millimetre and specimens placed in 10% formalin. Sex was determined from preserved specimens which were at least 115 mm long. Differentiation of gonadal sex is more easily distinguished after marked ovarian growth which occurs for landlocked sea lamprey larvae between 105 and 115 mm (Hardisty 1960).

Small feeding juveniles were taken from trap nets set by commercial fishermen in the lakes of the St. John River system and from the fishway at the Mactaquac Dam and hydroelectric installation (Fig. 1). Early upstream migrants were taken also from trap nets, particularly those set in Washademoak Lake (Fig. 1), while nearly mature and spent animals were captured from the fishway at Mactaquac and from the Keswick River, respectively. After anesthetization, lengths and generally also the weights were measured to the nearest millimetre and milligram in the case of feeding juveniles and 100 mg in upstream migrants. After animals had been preserved for a few days in 10% formalin sex and gonad weight were determined. Ovaries from nearly mature animals were placed in Gilson's fluid (Simpson 1951) for 7 wk after which fecundity was estimated from the relationship between the number of eggs in two subsamples each of approximately 1 g and that of the total weight of all eggs weighed at that time.

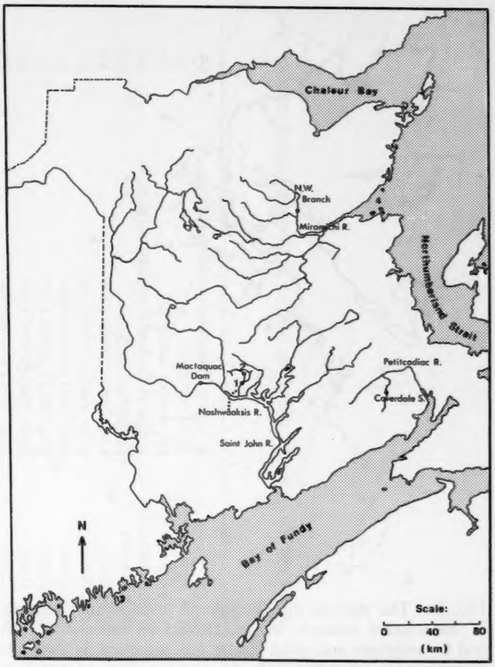

FIG. 1. New Brunswick showing the location of the two principal ammocoete sampling sites on the Nashwaaksis River, a tributary of the St. John River and the single sites on the Miramichi and Petitcodiac rivers and location of the Mactaquac Dam.

Information on the incidence and site of attachment or scarring attributable to juvenile sea lampreys was obtained from fish captured by trap nets set in Washedomoak Lake (Potter and Beamish 1977). Additional information on the species of fish attacked by sea lampreys in freshwater was obtained from questionnaires distributed to state, provincial, and federal governmental agencies in the United States and Canada. The questionnaires also provided information on the approximate length of sea lampreys in freshwater and the month during which the observations were made.

A total of 44 000 Atlantic salmon, *Salmo salar*, captured in the fishway at Mactaquac by Dep. Fisheries and Oceans were examined for length, weight, sex, and the presence and location of lamprey scars and other marks between 1972 and 1975.

The presence or absence of spawning size sea lamprey and the months in which they spawn in most rivers tributary to the Western Atlantic between Labrador and South Carolina were obtained from the questionnaires as well as some information on the effects of barriers or dams on the

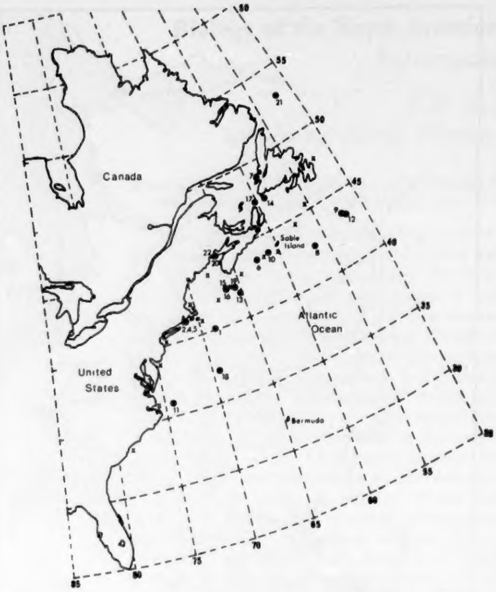

FIG. 2. The marine distribution of juvenile sea lamprey in the western Atlantic Ocean. Details on captures identified by numbers and solid circles are provided in Table 1. Capture sites identified only by a cross were reported in Bigelow and Schroeder (1948) without further detail.

spawning migration, the presence of landlocked populations of *P. marinus*, and the numerical size of spawning populations.

Marine Distribution of Juvenile Sea Lamprey

The geographical range of the sea lamprey in the Atlantic Ocean adjacent to North America is known to extend from a northern latitude of 53° off the coast of Labrador, southward to Florida at a latitude of approximately 30°. Sea lampreys occur in highest densities between latitudes of 35–45° (Fig. 2). The most northerly record is represented by a single specimen of 910 g captured in a bottom trawl set during August, 1977 at a depth of 247 m (Table 1). Reports of *P. marinus* from the waters off Greenland (Nordgaard 1927; Jensen 1926, both reported in Bigelow and Schroeder 1948) indicates the species is occasionally found north of the recorded range for eastern North America. Adult anadromous sea lampreys in the St. Johns River system of northern Florida (Evermann and Kendall 1900) defines the southern range for the species. Curiously, sea lampreys have not been reported from the coastal waters of Georgia, the state immediately to the North of Florida.

Sea lampreys when encountered in salt water are usually observed in shallow water near the coast or even in estuarine situations (Bigelow and Schroeder 1948, 1953), particularly small individuals under 400 mm in length (Fig. 2, Table 1). Small juveniles have been captured in pound and trap nets and in herring weirs set in shoal coastal water (Breder 1923, 1931; Hubbs 1925). Observations have been made also of small juvenile sea lamprey attached to pelagic fish swimming near shore in shoal water (Mansueti 1962; R. Cook, Dep. Fisheries and Oceans, St. Andrews, N.B., personal communication).

The presence offshore of small lampreys at depths to approximately 200 m is suggested by records of their capture in association with catches of demersal fishes made by otter trawl (Dep. Fisheries and Oceans, Table 1). Lampreys taken by benthic trawls are assumed to have been captured when they were on or near the sea bed. However, it is possible that those lampreys captured by otter trawl actually entered the net at some depth between the surface and bottom as it was being set or lifted. Certainly the depth of capture is less clear in diagonal hauls. Thus, a sea lamprey of 650 mm in length was taken in an Isaac-Kidd trawl towed upwards in a diagonal direction from 675 m approximately 160 km east of the coast of Nova Scotia (D. Kulka, Dep. Fisheries and Oceans, St. Andrews, N.B., personal communication). Large feeding juvenile sea lampreys have been captured most frequently offshore in deep water (Table 1). Research cruises operated by Dep. Fisheries and Oceans have recorded the capture of sea lampreys (580–650 mm long) in offshore waters at depths of 283–645 m.

The vertical depth range inhabited by sea lampreys is among the greatest exhibited by marine animals. Gill (1884, cited in Bigelow and Schroeder 1948) reported the capture of a 275 mm sea lamprey from 1000 m, approximately 145 km southeast of Nantucket. By far the greatest depth from which a sea lamprey has been captured is 4099 m (Haedrich 1977). The specimen 395 mm long, was taken in a shrimp trawl fished on bottom about 400 km off the southern New England coast.

Constraints imposed by temperature on the distribution of sea lampreys are not known. The species is tolerant of temperature within the range of −0.6 (Table 1) to at least 20°C (Potter and Beamish 1977; Beamish 1979). Neither the preferred nor lethal temperature (Fry 1947) has been determined for the marine phase sea lamprey. The ultimate incipient lethal temperature for ammocoetes of the landlocked sea lamprey, 31.4°C (Potter and Beamish 1975) is suggestive of a broad temperature tolerance for the species.

Reproduction

Following a period of feeding in salt water, sea lampreys migrate into rivers, construct nests, spawn and shortly thereafter die. Spawning sea lampreys have been recorded from the St. Johns River in Florida (Bigelow and Schroeder 1948), northward to streams tributary to the Bay of Chaleur (Fig. 3, 4, and 5). Not all of

TABLE 1. The marine distribution of sea lamprey in the western Atlantic Ocean. A number of capture locations were not identified specifically by latitude and longitude but rather by coastal landmarks, islands, or bays. Weights and lengths given in parentheses were calculated from a regression describing the general relationship between total length and wet body weight.

Date	Length (mm)	Weight (g)	Location		Depth (m)	Temperature	Capture technique	References	Identification on map
			Latitude	Longitude					
1883	275	(31)	40°	68°30′[a]	985			Gill (1883)[b]	1
May 11, 1923	430	(123)	41°30′	71°20′[a]			pound net	Breder (1923)	2
	137	(4)	37°40′	76°20′[a]				Hubbs (1925)	3
June 3, 1929			41°30′	71°20′[a]			pound net	Breder (1931)	4
June 5, 1929			41°30′	71°20′[a]			pound net	Breder (1931)	5
Mar. 21, 1936			43°50′	62°25′	157		otter trawl	Vladykov (1936)	6
July 1952	561	(276)	48°40′	58°10′[a]			trap net	Fish. and Oceans Can.[c]	7
May 25, 1957	181	(9)	42°30′	56°10′[a]			otter trawl	Fish. and Oceans Can.	8
Oct. 20, 1962	650	(433)	43°56′	52°41′	645	3.9	otter trawl	Fish. and Oceans Can.	9
Nov. 29, 1966	580	(306)	43°13′	61°01′	360	4.6	otter trawl	Fish. and Oceans Can.	10
Apr. 4, 1967	200	(12)	36°29′	74°43′	101		Isaac-Kidd trawl	Fish. and Oceans Can.	11
Nov. 25, 1967	624	(382)	43°42′	52°15′	283	7.5	otter trawl	Fish. and Oceans Can.	12
Mar. 20, 1970	300	(41)	42°25′	65°38′	95	4.9	otter trawl	Fish. and Oceans Can.	13
Feb. 22, 1973	(388)	90	47°30′	59°08′	192	3.0	otter trawl	Fish. and Oceans Can.	14
Feb. 21, 1975	195	(11)	42°37′	66°19′	126		otter trawl	Fish. and Oceans Can.	15
Feb. 21, 1975	315	(48)	42°37′	66°19′	126		otter trawl	Fish. and Oceans Can.	16
May 22, 1975	220	(16)	47°27′	60°27′	139	−0.6	otter trawl	Fish. and Oceans Can.	17
Apr. 24, 1976	395	75	37°32′	69°54′	4099		shrimp trawl	Haedrich (1977)	18
May 1, 1977	650	560	42°01′	65°10′	0–675		Isaac-Kidd trawl	Kulka (personal communication)[f]	19
July 26, 1977	354	(68)	45°03′	67°05′			herring weir	Huntsman museum[d]	20
Nov. 11, 1977	(829)	910	53°01′	52°22′	247	3.1	otter trawl	Environ. Can.	21
Aug. 24, 1978	300	(41)	45°03′	67°05′	0			R. Cook (personal communication)[e,f]	22

[a] Latitude and longitude estimated.

[b] Cited in Bigelow and Schroeder (1948).

[c] Catch records of Fisheries and Oceans Canada: Bedford Institute of Oceanography, Dartmouth, Nova Scotia; Biological Station, St. Andrews, New Brunswick; and Biological Station, St. John's, Newfoundland.

[d] Huntsman Marine Laboratory Museum, St. Andrews, N.B.

[e] Observed near surface attached to Atlantic salmon.

[f] Fisheries and Oceans Canada, St. Andrews, N.B.

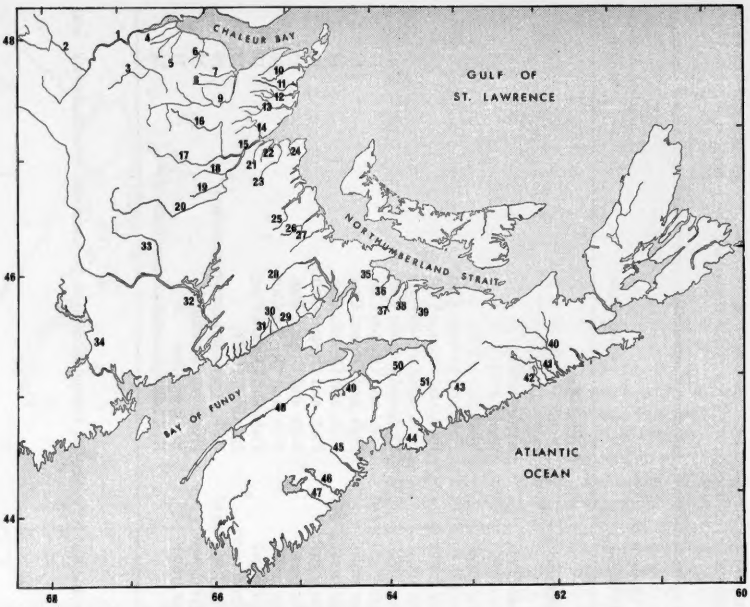

FIG. 3. Rivers and their tributaries which support spawning migrations of anadromous sea lampreys in New Brunswick and Nova Scotia. Spawning migrations have not been reported from Prince Edward Island. Names of rivers identified in the figure by numbers are: *New Brunswick* — 1, Restigouche; 2, Kedgwick; 3, Upsalquitch; 4, Eel; 5, Charlo; 6, Jacquet; 7, Tetagouche; 8, Middle; 9, Nepisiguit; 10, Pocemouche; 11, Little Tracadie; 12, Big Tracadie; 13, Tabusintac; 14, Bartibog; 15, Miramichi; 16, Northwest Miramichi; 17, Little Southwest Miramichi; 18, Renous; 19, Bartholomew; 20, Southwest Miramichi; 21, Napan; 22, Black; 23, Bay du Vin; 24, Eel; 25, Coal Branch; 26, Buctouche; 27, Cocagne; 28, Petitcodiac; 29, Goose; 30, Quiddy; 31, Big Salmon; 32, St. John; 33, Nashwaak; 34, St. Croix; *Nova Scotia* — 35, Tidnish; 36, Shinimecas; 37, Philip; 38, Pugwash; 39, Wallace; 40, St. Mary's; 41, Gaspereau; 42, Ecum Secum; 43, Musquodoboit; 44, Nine Mile; 45, La Have; 46, Medway; 47, Mersey; 48, Annapolis; 49, Gaspereau; 50, Kennetcook; 51, Shubenacadie.

the rivers within this range are used by migrant lampreys. The questionnaires distributed to fishery agency personnel indicate the presence of spawning size sea lampreys in 116 rivers between approximately 32 and 48° latitude (Fig. 3, 4, and 5). Ammocoetes have been collected from 28 other rivers in which spawning adults were not observed. It is suspected that lampreys use other rivers; however, ammocoetes or adults have not been observed. Reports were not received of adult sea lampreys in rivers south of North Carolina although Bigelow and Schroeder (1948) identified the Savannah and Pee Dee Rivers in South Carolina and the St. Johns River in northern Florida as spawning sites. Northward, spawning lampreys have not been observed in the rivers of Newfoundland, Labrador or Prince Edward Island. Reports from Quebec were sufficiently incomplete as to be of little assistance to the survey. A study conducted by Vladykov (1952) on the distribution of ammocoetes indicates that sea lampreys use some of the streams in Quebec tributary to the St. Lawrence River.

The reasons why lampreys migrate into a river are not known although temperature and discharge appear to be important for at least the landlocked form (Applegate 1950; Wigley 1959; Beamish and Potter 1975). A correlation has been found between the number of lampreys migrating at a given time and water temperature of the river (Applegate 1950). Among the landlocked sea lampreys, upstream migration seldom occurs at temperatures under 4.5°C and is most active between 10 and 18.5°C. Temperatures above these levels are thought to reduce migration and spawning intensity. A similar pattern appears to occur among the anadromous sea lampreys. Spawning activity in the Keswick River, a tributary of the St. John River, New Brunswick appears to reach a maximum during the

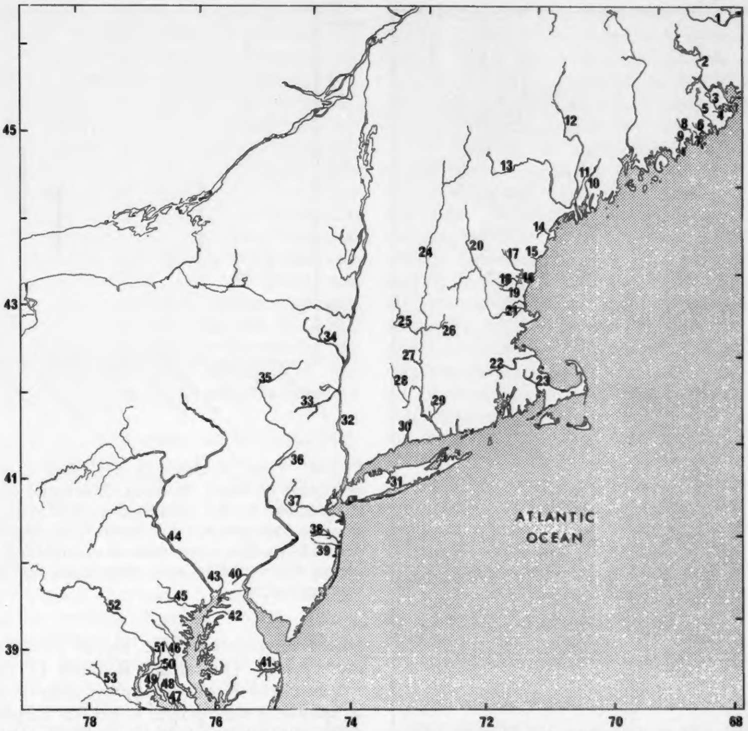

FIG. 4. Rivers and their tributaries which support spawning migrations of anadromous sea lampreys from New Brunswick to Virginia. Names of rivers identified in the figure by numbers are: *New Brunswick* — 1, St. John; *Maine* — 2, St. Croix; 3, Dennys; 4, Hobart; 5, East Machias; 6, Chandler; 7, Indian; 8, Pleasant; 9, Tunk; 10, Sheepscot; 11, Eastern; 12, Kennebec; 13, Androscoggin; 14, Nonesuch; 15, Little River Wells; 16, Piscataqua; *New Hampshire* — 17, Cocheco; 18, Lamprey; 19, Exeter; *Massachusetts* — 20, Merrimack; 21, Parker; 22, North; 23, Weweantic; 24, Connecticut; 25, Deerfield; 26, Miller; 27, Agawam; *Connecticut* — 28, Farmington; 29, Salmon; 30, Quinnipiac; *New York* — 31, Nissequogue; 32, Hudson; 33, Rondout; 34, Catskill; 35, Delaware; *New Jersey* — 36, Flat; 37, Raritan; 38, Manasquan, 39, Metedeconk; *Delaware* — 40, Christina; 41, Indian; *Maryland* — 42, Fairlee; 43, Northeast; 44, Susquehanna; 45, Gunpowder; 46, Patuxent; 47, St. Clement; 48, Wicomico; 49, Port Tobacco; 50, Mattawoman; 51, Piscataway; 52, Potomac; *Virginia* — 53, Rappahannock.

latter part of June and early July when water temperature ranges between 17 and 19°C. The proportion of migrant sea lampreys returning to their natal stream is unknown for the anadromous or freshwater form.

Spawning migrations by anadromous sea lampreys occur between March and September. Generally, the time of the upstream movement varies directly with latitude, the earlier migrations tending to occur in streams at the lower latitudes. In North Carolina, the main period of migrational activity occurs in March with some activity extending through to August (Fig. 6). Migrations in Virginia and Maryland occur between March and June with reproduction reaching a maximum in April and May. In Massachusetts most migrant lampreys spawn in May and June whereas in New Brunswick the main activity occurs in mid-June to early July with some reproduction reported as late as September. Specific information on the precise timing of the migration and period of spawning is not recorded for most rivers. It is likely that these periods are influenced not only by temperature and latitude but also by the distance between the estuary and the spawning site. The St. John River in New Brunswick runs approximately 756 km from its source in northern Maine to its estuary which discharges into the Bay of Fundy. Beamish (1979) estimated that lampreys

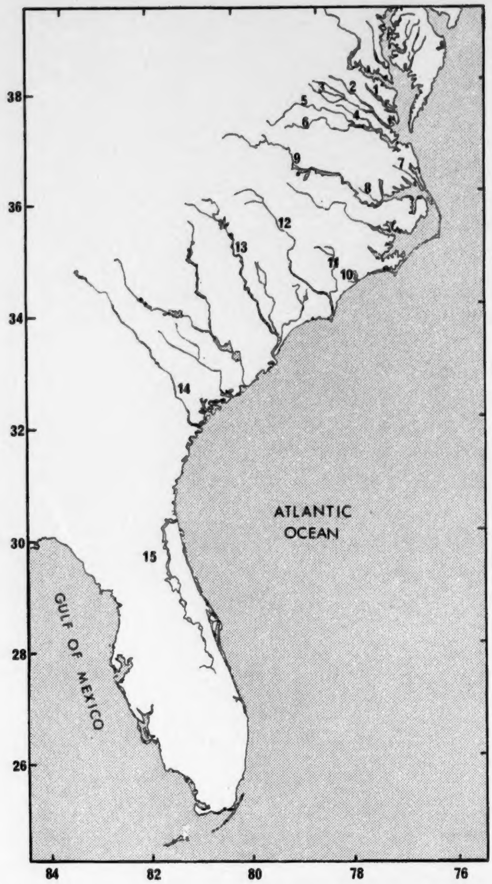

FIG. 5. Rivers and their tributaries which support spawning migrations of anadromous sea lampreys from Virginia to Florida. Names of rivers identified in the figure by numbers are: *Virginia* — 1, Rappahannock; 2, Mattaponi; 3, Pamunkey; 4, Chichahominy; 5, James; 6, Appomattox; *North Carolina* — 7, North; 8, Cashie; 9, Roanoke; 10, Mill; 11, Northeast Cape Fear; 12, Cape Fear; *South Carolina* — 13, Pee Dee; 14, Savannah; *Florida* — 15, St. Johns.

first enter this river in early April with maximum spawning activity at a site approximately 140 km upstream from the estuary occurring between late June and early July. Spawning lampreys have been observed breeding at least 1 wk earlier in small tributaries in the downstream sections of the St. John River than further upstream. This suggests that individuals move into suitable spawning areas when they attain a certain stage of maturity or that on entering the smaller tributaries

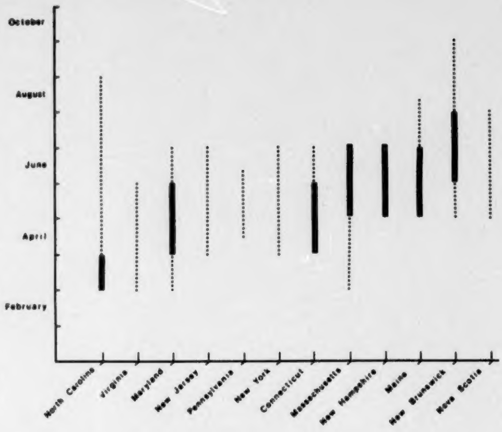

FIG. 6. Time of spawning migrations in rivers along the east coast of North America. Maximum spawning activity is indicated by the thickened vertical lines. The information for Pennsylvania was taken from Bigelow and Schroeder (1948). The other data were provided from questionnaires distributed to state provincial, and federal government agencies.

where temperatures are higher they reach maturity more rapidly (Potter and Beamish 1977).

The distance which lampreys migrate upstream prior to spawning may extend to several hundred kilometres. Spawning lampreys have been found in the upper reaches of the Dalaware and Susquehanna River systems approximately 320 km from the sea (Bigelow and Schroeder 1948). In the Savannah River lampreys have been observed spawning 240 km upstream from the estuary. The upstream migration by sea lampreys in the St. John River is now restricted by a dam to 140 km from the estuary, but it once extended further upstream.

The number of migrating lampreys has not been documented for most rivers along the east coast of North America. Of those rivers for which recent estimates are available by far the largest migration is that in the Connecticut River (P. Coates, Dep. Fisheries, Wildlife and Recreational Vehicles, Massachusetts, personal communication). The number of sea lampreys which annually ascend this river has been estimated at more than 50 000 individuals. Approximately 8600 sea lamprey were captured at the Mactaquac Dam when it was first made functional and this is considered a conservative estimate of the total number which enter this river. Many of the rivers which discharge into the main stem of the St. John between the estuary and the dam serve as spawning sites for migrating lampreys. It is likely that the total number of lampreys which annually enter the St. John exceeds that taken at the Mactaquac Dam by at least an order of magnitude. In the much smaller Sheepscot River, Maine, the annual run of migrating lampreys has been estimated at 3000–8000 individuals (L. H. Bond, Dep. Inland Fish and Game, Maine, personal communication). Davis (1967) captured by trap net all migrant lampreys entering Barrows Stream, a tributary of the Machias River, Maine between 1960 and 1964. The average annual catch excluding 1961 when high water prevented the operation of the trap net for 4 wk was 14 individuals. The range among years was one to 24 sea lampreys. Fifteen trap nets set in the Buctouche River, New Brunswick, for American eel, *Anguilla rostrata*, captured approximately 100 sea lampreys daily during their upstream migration (P. H. Sutherland, Dep. Fisheries and Oceans, Halifax, N.S., personal communication). Neither the efficiency of the trap nets nor the exact length of the spawning migration is known for the Buctouche River. However, even conservative estimates suggest an annual run of several thousand sea lampreys.

The sex ratio of spawning phase sea lampreys indicates a slight preponderance of males. In a collection of 456 adults caught in the fishway at the Mactaquac Dam between mid-May and early July, 1975, 1976, and 1977, the ratio of females to males was 1:1.36 (Beamish et al. 1979). On the basis of the much smaller sample of 66 animals collected over a 5-yr period Davis (1967) reported a ratio of females to males of 1:1.90 for those migrants entering Barrows Stream, Maine. These ratios are similar for samples of landlocked spawning phase sea lampreys collected in five successive years from the Humber River, a tributary of Lake Ontario (Potter et al. 1974). The slight excess of males is likely typical for populations which have been established for a long time and suggests that male lampreys have a more variable reproductive success than females.

The size of the nontrophic migrant sea lamprey is highest early in the upstream movement and decreases as individuals reach maturity. Beamish (1979) suggested sea lampreys enter the St. John River early in April at which time the mean length and weight for both sexes was estimated to be about 830 mm and 925 g. The earliest lampreys were captured in the St. John during mid-May at a site 80 km upstream from the estuary. At this time mean length and weight of females was 773 mm and 896 g, respectively. Approximately 35 d later at a site 60 km further upstream length and weight of nearly mature females was 729 mm and 885 g (Beamish et al. 1979). Only a few days later following the release of the gonadal products, length and weight of females was 628 mm and 645 g. The pattern followed by males was similar to that for females; however, values for the early migrant and nearly mature stages were higher for females. Length and weight loss by females after spawning was significantly greater than that for males. These reductions in length and weight which are expressions of synchrony (Mislin 1941) were described first in lampreys by Contronei (1924a, b, 1926). If it is assumed that the lampreys caught in mid-May are part of the same population that was captured in late June 60 km further upstream and just prior to spawning in a nearby stream, these length data can provide an estimate of the relative degree of shrinkage that occurs during the spawning migration. Thus in females, length declined by 5.7% between mid-May and late June and a further 13.9% between the latter sample and the completion of the short maturation and reproduction phase. In the males the corresponding values are 5.7 and 6.6%, the latter considerably lower than that found for females, a feature similar to that described by Larsen (1973) for river lampreys, *Lampetra fluviatilis*. The overall decrease of 18.8 and 12.0% between the early upstream migrant and spent females and males, respectively, are only marginally above the values of 17.9 and 11.0% found by Wigley (1959) for comparable stages of the landlocked form in Cayuga Lake. It should be emphasized that the total shrinkage between the first entry into freshwater and spawning is almost certain to be greater than that calculated for lampreys after they had been migrating for more than a month. Based on an estimated length of 830 mm for very recent anadromous migrants the total shrinkage to the completion of spawning is 24.3 and 18.6% for females and males, respectively.

The gonadosomic ratio of migrant males is below that of females for comparable stages in the upstream movement in the St. John River (Beamish et al. 1979). Between the early migrant and nearly mature interval the gonadosomic ratio of females increased for 11.2–16.8% whereas that for males decreased from 2.2 to 1.3%.

Fecundity of the anadromous sea lamprey does not correlate with either length or weight on the basis of 40 specimens collected from the St. John River (Beamish and Potter 1975) and 10 specimens from Quebec (Vladykov 1951). Failure to demonstrate a correlation with length or weight at least for animals from the St. John may have been influenced by the variability in the developmental stage of the gonads. The mean number of eggs for females from the St. John was 210 228 with a range of 151 836–304 832. In contrast, Vladykov (1951) found a mean of 171 589 with a range of 123 873–258 874 for animals from Quebec. The egg counts for anadromous sea lampreys are the highest recorded for any lamprey species (Hardisty 1971). In terms of relative fecundity (i.e. number of eggs $(\text{body weight})^{-1}$), the anadromous sea lamprey had a mean of 233 (range of 142–387), lower than that found in all other species and in particular those of the non parasitic lampreys (Hardisty 1964).

Energy requirements for the spawning migration and maturation of the gonads are derived exclusively from the catabolism of products stored during the marine feeding phase. In this context, Nikol'skii (1963) suggested that the amount of lipid, the principal energy source, deposited by lampreys prior to the migration is related to the distance that a particular species must travel to the spawning grounds. The amount of lipid accumulated by lampreys appears also to vary with the duration of the migration (Lanzing 1959; Moore and Potter 1976; Beamish et al. 1979). The expenditure of energy displayed for breeding by sea lampreys from the St. John River was considerably greater than that catabolized during the migration (Beamish 1979). Energy utilization for the entire migration of 140 km was estimated at not more that 1.256 and 1.046 kJ for males and females, respectively.

The metabolic expenditure by males in nest construction and the vigorous locomotory activity associated with breeding represented 1.846 kJ. Apart from the loss of ovarian products, females expended 1.762 kJ in spawning. The slightly greater parental investment in terms of energy expenditure for breeding exhibited by males is consistent with the general observation that they play a more active role in spawning than females. On completion of spawning, the total energy content of males and females was remarkably similar and about one half of that in early upstream migrants. While depletion of energy in spent sea lampreys was severe, relative values of proximate body constituents were in all cases greater than those found for small lampreys which had just begun to feed subsequent to the completion of metamorphosis. It would seem therefore that the natural death which follows spawning may not be mainly attributable to the depletion of stored energy.

Ammocoetes

The duration of the larval phase of anadromous *P. marinus* has been estimated for several river populations from New Brunswick (Beamish and Potter 1975). Estimates were based on length-frequency distribution in concert with information on the time of spawning and metamorphosis. Attempts to assign length ranges to individual age-classes are always uncertain because of the variability in ammocoete growth rates from neighbouring localities within the same river (Hardisty 1944; Potter 1980). Spawning in the rivers studied occurred during the latter part of June and early July. The lengths of the 0 year-class, and the time of their first appearance in samples was consistent with a spawning season restricted to this period. A comprehensive examination of anadromous sea lampreys in Dennis Stream, New Brunswick by Potter et al. (1978) indicates that metamorphosis begins during early to mid-July and ends by mid-October.

Length frequency curves for ammocoetes collected from two sites on the Nashwaaksis River (Fig. 7) on July 20, 1972 showed five peaks with that corresponding to the smallest individuals occurring at approximately 40 mm. These collections also contained several metamorphosing animals (average 143 mm). By late July the 0 class had not yet entered the typical ammocoete substrate. Thus, the peaks in the frequency curves are suggestive of five year-classes, with the metamorphosing animals corresponding to year-class VI. The presence of some ammocoetes in excess of 150 mm suggests that at least some animals spend an additional year as an ammocoete (O'Boyle and Beamish 1977). Comparison of the year-class length from the two sites suggests that larvae of age III and IV from site 2 were exposed to more favorable conditions for growth during their early life than those from the downstream location. Samples from the Miramichi River provided a pattern approximately intermediate between the upstream and downstream locations on the Nashwaaksis.

The duration of larval life in the Petitcodiac River is in general agreement with that for both the Miramichi and Nashwaaksis rivers (Fig. 7). The modes corresponding to year-classes I, III, IV, and V can be distinguished in the sample from July 28, 1973 with a much smaller distribution representing year-class II. Most of the modes can be traced with reasonable certainty through the subsequent September and November samples into the following June.

From the New Brunswick data there is evidence for the view that the most clearly defined peak at the upper end of the length-frequency curves for samples taken from the Petitcodiac between late July 1973 and May 1974 correspond to year-class V. These lampreys would become year-class VI in late June at the time of spawning. On the evidence of the size of metamorphosing individuals, some of these year-class VI lampreys would likely have commenced metamorphosis in July. The capture of a metamorphosing animal of 163 mm in September and the presence in some of the samples of a number of animals whose lengths lie to the right of the distribution corresponding to year-class V, suggest that metamorphosis is likely delayed in some members of the population until the commencement of the seventh year of larval life.

Evidence has been presented to suggest that at least some ammocoetes exhibit little or no growth during the final year of larval life when they alter metabolic pathways to provide for an increased deposition of lipid at the expense of protein prior to the lengthy nontrophic phase of metamorphosis (Hardisty and Potter 1971; Lowe et al. 1973; O'Boyle and Beamish 1977). On this basis it is likely that some of the animals estimated as requiring 6 or 7 yr to reach metamorphosis, might take one additional year. Despite the difficulties at the upper end of the length range, the data do provide a strong indication that a reasonable proportion of the population transform at the beginning of their sixth, seventh, or possibly even eighth year of life. MacDonald (1959) estimated the duration of larval life to be 5 yr for the anadromous sea lamprey in Scotland while Hardisty (1969b) suggests it to be at least 5 yr for animals captured in English streams. It is clear from Hardisty's data that the pattern of growth in the British populations he investigated is remarkably similar to that found in New Brunswick.

Algae, primarily diatoms, were the organisms most frequently found in the intestinal tract of larval

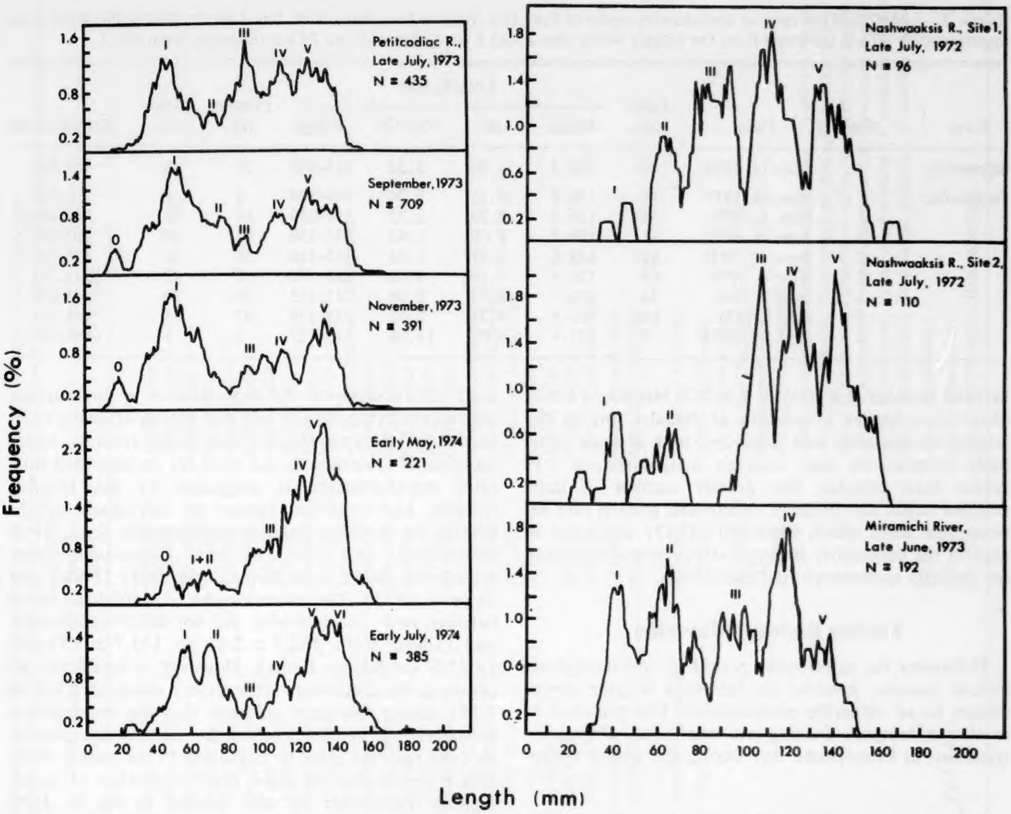

FIG. 7. Length–frequency curves for samples of ammocoetes from three rivers (see Fig. 1). Data are smoothed by moving averages of seven (Taylor 1965). Sample size is indicated by *N* (redrawn from Beamish and Potter 1975).

anadromous sea lampreys (Moore and Beamish 1973). Aside from algae, the protozoan *Diflugia* was the most frequently encountered organism. The relative abundance of organisms in the gut was similar to that in samples of sediment and water suggesting that ammocoetes are not selective feeders provided the particle is not too large to be ingested.

Differentiation of the gonad in larval sea lampreys is particularly difficult to recognize among individuals below 90 mm in total length (Hardisty 1960). Identification of ammocoete sex is more certain with ovarian growth which becomes marked at lengths of 105–115 mm (Hardisty 1960). Sex of larval sea lampreys collected from the Miramichi and Petitcodiac rivers, New Brunswick was determined for individuals measuring 115 mm or more in total length. Of 476 animals examined (Fig. 8, Table 2), females were more abundant than males with a ratio of 1 female to 0.731 males. The sex ratio varied between the two rivers and among the localities and seasons in samples from the Petitcodiac River. However, in most cases there was a preponderance of females.

Examination of sex ratios by length-class intervals of 5 mm showed an excess of females for all ammocoetes above 125 mm (Fig. 8). The higher proportion of males in the shorter length-classes may reflect an error in distinguishing between ovary and testis. In this regard Hardisty (1964) found oocyte growth from a small sample of the British anadromous sea lamprey to occur at a larger size than was observed for the North American landlocked *P. marinus*. The pattern of the relationship between ammocoete numbers and length class for individuals of 125–150 mm in total length was identical for both sexes with the number of females being approximately twice that of males. This is reflected in the overall sex ratio of the larger ammocoetes which was one female to 0.571 males ($n = 338$). In accord, Hardisty (1965) found an excess of females among ammocoetes collected from several British streams. The overall ratio based on 512 animals

TABLE 2. Length and sex ratio of ammocoetes captured from two rivers in New Brunswick. Site 1 on the Petitcodiac River was approximately 40 km upstream from the estuary while sites 2 and 3 were about 16 and 24 km upstream from site 1.

				Length, mm						
River	Site	Date	Total (*n*)	Mean	SD	95% CL	Range	Female (*n*)	Male (*n*)	Female:male
Miramichi		June 14, 1973	47	128.4	11.03	3.22	115–161	31	16	1:0.516
Petitcodiac	1	June 28, 1973	10	126.9	10.13	7.24	115–144	4	6	1:1.500
	1	Nov. 6, 1973	41	129.3	8.72	2.75	115–156	13	28	1:0.464
	2	June 28, 1973	71	129.7	8.09	1.92	115–150	42	29	1:0.691
	2	Sept. 11, 1973	81	128.6	8.27	1.84	115–148	58	23	1:0.397
	2	Nov. 6, 1973	65	129.9	7.19	1.78	115–150	38	27	1:0.711
	2	May 7, 1974	74	130.7	8.95	2.08	115–153	40	34	1:0.850
	2	July 1, 1974	84	135.6	9.71	2.12	115–159	47	37	1:0.787
	3	Sept. 13, 1978	3	121.3	6.03	14.98	115–127	2	1	1:0.500

favored females at a ratio of 1:0.772. Hardisty (1965) observed a higher proportion of females among the largest ammocoetes and suggested that at least some male ammocoetes may undergo metamorphosis 1 yr earlier than females. The greater number of large females might also reflect a differential growth rate between the sexes which Churchill (1945) suggested to explain the bimodality in length–frequency distribution for recently metamorphosed individuals.

Feeding Ecology of Juveniles

Following the nontrophic period of metamorphosis in late autumn, juvenile sea lampreys migrate downstream to an estuarine environment. The presence of small sea lamprey feeding on menhaden, *Brevoortia tyrannus*, in Chesapeake Bay during the winter (Mansueti 1962) supports the suggestion of a downstream migration during the late autumn shortly after the completion of metamorphosis. That some recently metamorphosed lampreys do not feed for an extended time after transformation is suggested by the lengths, weights, and condition factors of individuals caught feeding on alewife, *Alosa pseudoharengus*, shad, *Alosa sapidissima*, and white suckers, *Catostomus commersoni* in the St. John River during May (Potter and Beamish 1977). The mean lengths of individuals taken between mid- and late-May did not differ significantly and ranged from 132.7 ± 2.81 to 135.7 ± 3.71 mm (±95% confidence limits). However, a significant increase in the condition factor from a mean of 1.115 to 1.353 during this time indicates that the short period spent feeding in May enables the animal to replenish its food reserves prior to migrating to the ocean. Fishermen report that in some years a number of larger feeding individuals are also present in the St. John River. In 1975 six specimens were collected in May, having a mean length of 211 ± 48.6 mm. Two larger feeding sea lampreys (242 and 292 mm) were also caught in early June near the mouth of the river. These eight specimens had obviously been feeding longer than the majority of the river population. Potter and Beamish (1977) suggest that in the St. John River system newly metamorposed lampreys move downstream during either late autumn or spring subsequent to peak water levels. Such a variation in the time of onset of feeding and migration is consistent with the fact that in a coastal Maine lake, Davis (1967) recorded two main periods when lampreys were feeding, October–February and May–June and also found that between the autumn and following May the length of the downstream migrants ranged from 127 to 234 mm, the latter length being well in excess of the maximum size that would be expected during metamorphosis. The suggestion of a spring downstream migration by metamorphosed sea lampreys facilitated by a brief feeding period following an extended nontrophic interval is concordant with observations reported for several east coast rivers and freshwater lakes (Table 3). In these rivers lampreys

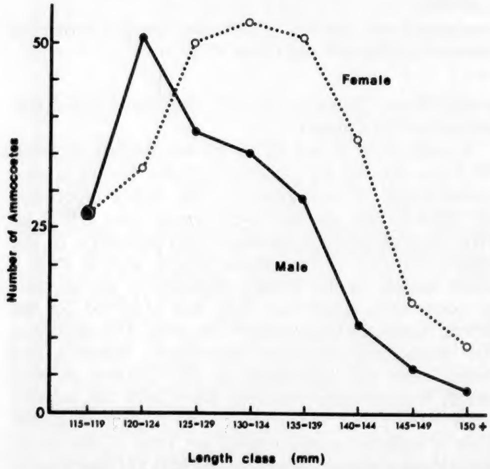

FIG. 8. Frequency distribution of male and female sea lamprey ammocoetes by length-class, collected from the Miramichi and Petitcodiac rivers, New Brunswick.

TABLE 3. Reported attachments by sea lampreys in North American rivers tributary to the Western Atlantic Ocean.

Country	River	Observation period	Sea lamprey length (mm)	Host species
Canada				
New Brunswick	Bain	Aug.–Sept.	380–400	*Salmo salar*
	Big Salmon	Aug.–Oct.	380–400	*Salmo salar*
	Black	Aug.	380–400	*Salmo salar*
	Gardner Cr.	Aug.Sept.	380–400	*Salmo salar*
	Goose	Aug.–Sept.	350–400	*Salmo salar*
	Irish	Aug.–Sept.	350–400	*Salmo salar*
	Kedgwick	June	200–300	*Salmo salar*
	Little S.W.	June–July	250–350	*Salmo salar*
	Little Salmon	Aug.–Sept.	380–400	*Salmo salar*
	Mosher	Aug.–Sept.	350–400	*Salmo salar*
	N.W. Miramichi	July	250–350	*Alosa sapadissima, Salmo salar*
	Restigouche	June	200–300	*Salmo salar*
	Quiddy (Martin Head Str.)	Aug.–Sept.	250–350	*Salmo salar*
	Upsalquitch	June	200–300	*Salmo salar*
	Eel	Aug.	250–450	*Salmo salar*
	Jacquet	Aug.–Sept.	300–400	*Salmo salar*
Nova Scotia	Annis	Apr.–May	150–180	*Alosa pseudoharengus*
	Argyle	Apr.–May	150–180	*Alosa pseudoharengus*
	La Have (Sherbrooke Lk.)	May–June	100–200	*Salvelinus namaycush*
	Liscombe	Aug.	300–380	*Salmo salar*
	Stewiacke	autumn	—	*Salmo salar*
	St. Mary's	July–Aug.	200–380	*Salmo salar*
	Tusket	Apr.–May	150–180	*Alosa pseudoharengus*
Prince Edward Is.	Naufrage	summer	150–250	*Salvelinus fontinalis*
	Morell	summer	small	*Salvelinus fontinalis*
United States				
Maine	Little (Branch Bk.)	summer–autumn	200–250	*Salvelinus fontinalis*
Massachusetts	Connecticut	May–June	150–250	*Alosa sapadissima*
	Eel			*Alosa sapadissima*
	North		150–200	*Alosa sapadissima*
	Palmer		450	*Alosa sapadissima*
	Parker		200–300	*Alosa pseudoharengus*
Virginia	Appomattox			*Alosa sapadissima, Pomatomus saltatrix, Cynoscion regalis*
	Chickahominy			*Alosa sapadissima, Pomatomus saltatrix, Cynoscion regalis*
	James			*Alosa sapadissima, Pomatomus saltatrix, Cynoscion regalis*
	Mattaponi			*Alosa sapadissima, Pomatomus saltatrix, Cynoscion regalis*
	Pamunkey			*Alosa sapadissima, Pomatomus slatatrix, Cynoscion regalis*
	Rappahannock			*Alosa sapadissima, Pomatomus saltatrix, Cynoscion regalis*
North Carolina	Cape Fear		300[a]	*Alosa sapadissima*
South Carolina	Edisto	Feb.–Mar.	150–540	*Alosa sapadissima*
	Cooper		150–300	*Alosa sapadissima, Alosa aestivalis*

[a] Based on two specimens.

TABLE 4. Reported occurrences and estimated lengths of free-swimming sea lampreys in rivers tributary to the Canadian North West Atlantic Ocean.

Province	River	Observation period	Length (mm)
New Brunswick	Bain	Aug.–Sept.	350–400
	Bartholomew	July–Aug.	150
	Bay du Vin	June–Aug.	small
	Big Salmon	Aug.–Sept.	380–400
	Black	Aug.–Sept.	350
	Crooked Cr.	May–June	<600[a]
	Demoiselle	May–June	<600[a]
	Eel	June–Aug.	250–450
	Forty-five	May–June	<600
	Gardner Cr.	Aug.–Sept.	350
	Goose	Aug.–Sept.	360–400
	Irish	July–Sept.	360–400
	Jacquet	Aug.–Sept.	250–350
	Kedgwick	June–July	200–300
	Little Salmon	Aug.–Sept.	350–400
	Little S.W. Miramichi	June–Aug.	250–350
	Little Tracadie	Aug.–Sept.	small
	Mill	May–June	<600
	Mispec Cr.	Aug.–Sept.	250–350
	Mosher	Aug.–Sept.	350–400
	Nashwaak	June–July	150–200
	Nepisiguit	—	unspecified
	N.W. Miramichi	June–Aug.	250–350
	Pokemouche	Aug.–Sept.	small
	Restigouche	June–July	150–250
	Sawmill Cr.	May–June	<600[a]
	St. Croix	June-Aug.	200–250
	St. John	June–Aug.	250–400
	South Caraquet	June–Aug.	200–250
	Shepody	—	<600[a]
	Tabusintac	July–Aug.	500
	Tracadie	Aug.–Sept.	small
	Upsalquitch	June–July	200–300
	Weldon Cr.	May–June	<600[a]
	West	May–June	<600[a]
Nova Scotia	Ecum Secum	July–Aug.	300–380
	Gaspereau Br.	July–Aug.	300–380
	Philip	June	small
	St. Mary's	May–Sept.	200–600[a]
	Shinimecas	June	small
	Tidnish	June	small
	Wallace	June	small
Prince Edward Is.	Morell	summer	small

[a]May represent spawning migrants.

estimated to be approximately 150–180 mm in length were observed in April and May attached to alewife and shad.

That young juvenile lampreys commence feeding at different times is supported by the size variation of feeding *P. marinus* captured at the Mactaquac Dam. Sea lampreys captured at this site between late June and mid-July attached to Atlantic salmon ranged in length from 153 to 403 mm (Beamish et al. 1979). While this large variation in size may indicate the presence of more than one year-class it seems equally feasible that it is predominantly a reflection of differing times in the onset of feeding, a view suggested earlier by Applegate (1950) to account for similar variations in the size of juvenile landlocked sea lampreys. Among those rivers tributary to the Atlantic Ocean along the Canadian coast in which juvenile sea lampreys have been reported the size range is generally within that observed in the St. John River (Table 3 and 4).

Subsequent to the downstream migration, metamorphosed sea lampreys appear to remain largely within the confines of estuarine water or at least close to the

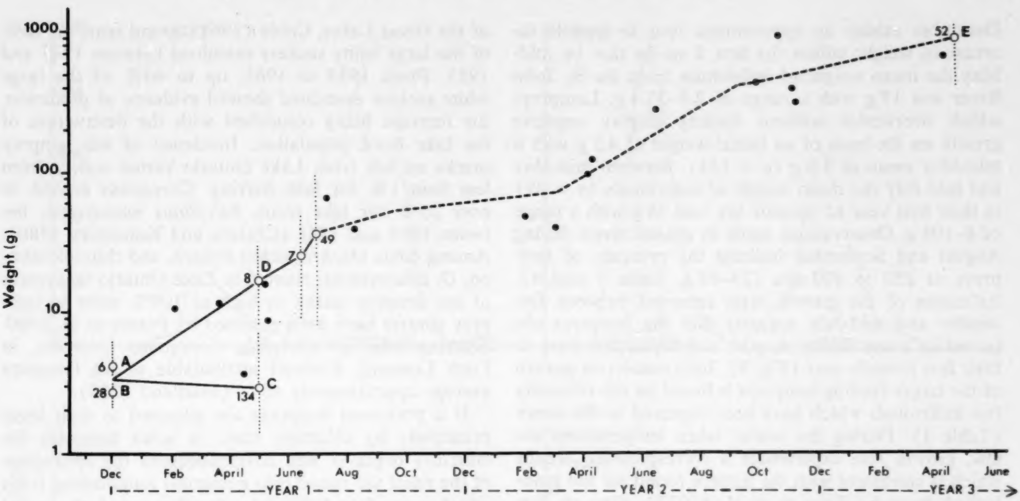

FIG. 9. A proposal of the growth of juvenile anadromous sea lampreys from the east coast of North America. Open circles denote the mean weight of a sample, the range being indicated by a vertical line. The sample size is given beside the open circle. Closed circles indicate individual values. The letter *A* denotes the mean weight of metamorphosed sea lampreys collected from the Petitcodiac and Nashwaaksis rivers and *B*, the mean weight of individuals from Dennis Stream (Potter et al. 1978). The mean weight of juveniles which overwintered after metamorphosis without feeding is indicated by *C*. The weight of juveniles presumed to have fed during the first winter following metamorphosis is designated by *D*. Nonfeeding early upstream migrants are denoted by *E*.

coast (Bigelow and Schroeder 1948, 1953). Mansueti's (1962) observation of small sea lampreys (153–173 mm) overwintering in Chesapeake Bay where the salinity is about 16‰ prompted the suggestion by Mathers and Beamish (1974) that the full osmoregulatory capacity of small juvenile *P. marinus* may not be realized for some time after their downstream migration. However, a recent study by Beamish et al. (1978) indicates that anadromous feeding sea lamprey of all sizes are able to osmoregulate in salinities between 0 and 34‰ in contrast to the landlocked form in which only the larger individuals could regulate above 16‰.

Small sea lampreys have been observed attached mainly to migrating anadromous teleosts in rivers (Table 3). The lengths of feeding juvenile sea lampreys in rivers is generally within the range of 150–400 mm. The occurrence of these feeding lampreys in rivers is assumed to result from attacks made on migrating teleosts in marine or estuarine waters. Unattached small sea lampreys are reported also in coastal rivers, presumably the result of detachments from their migrating host fish (Table 4).

Little information on the feeding ecology of sea lampreys in the marine environment is available because few specimens have been captured in the ocean and reports of scarred fish are scarce. Bigelow and Schroeder (1948, 1953) report that sea lamprey attack a variety of marine fish including basking shark, *Cetorhinus maximus*; sturgeon, *Acipenser* spp.; shad, *Alosa* spp.; herring, *Clupea* spp.; Atlantic salmon; Atlantic cod, *Gadus morhua*; haddock, *Melanogrammus aegelefinus*; pollock, *Pollachius virens; hake, Urophycis* spp.; and swordfish, *Xiphias gladius*. Comments received on questionnaires indicate sea lampreys also attack striped bass, *Roccus saxatilis*; bluefish, *Pomatomus saltatrix*; and weakfish, *Cynoscion regalis*.

Growth and duration of the juvenile feeding interval can be estimated from quantitative information on sea lampreys collected in fresh and salt water in concert with qualitative observations provided from the questionnaires completed by fishery officials. For the present purpose growth is defined as a change in wet body weight within a specified interval of time. Where only length was measured or estimated conversion to weight was calculated from a regression determined from measurements made on 248 feeding and nonfeeding early upstream migrant sea lampreys:

$$\log \text{weight (g)} = -5.9477 + 3.0518 \log \text{length (mm)};$$
$$r = 0.9546, \text{ significant at } P < 0.01.$$

The mean weight of a sample ($n = 28$) of recently metamorphosed sea lampreys from Dennis Stream, New Brunswick was 2.8 g with a range from 2.2 to 6.1 g (Potter et al. 1978), below the mean of 4.3 g found for a small sample of individuals ($n = 6$) from other rivers in the province (Beamish and Potter 1975; Fig. 9). Sea lampreys which commence feeding in

December exhibit an approximate four to six-fold increase in weight within the first 5 mo so that by mid-May the mean weight of individuals from the St. John River was 17 g with a range of 7.9–31.4 g. Lampreys which overwinter without feeding display negative growth on the basis of an initial weight of 4.3 g with a mid-May mean of 3.0 g ($n = 134$). Between mid-May and mid-July the mean weight of individuals ($n = 49$) in their first year of juvenile life was 38 g with a range of 8–104 g. Observations made in coastal rivers during August and September indicate the presence of lampreys of 250 to 400 mm (24–98 g, Table 3 and 4). Extension of the growth rates recorded between December and mid-July suggests that the lampreys observed in rivers during August and September were in their first juvenile year (Fig. 9). Information on growth of the larger feeding lampreys is based on the relatively few individuals which have been captured in the ocean (Table 1). During the winter when temperatures are low, growth rate experiences a corresponding decline which is consistent with the pattern found for the landlocked form by Farmer et al. (1977). Growth rate again increases with rising water temperatures during late spring, summer, and early autumn of the second year. It is suggested that the juvenile feeding interval is completed during the third winter when lampreys achieve their maximum weight. On this basis the feeding interval lasts between 23 and 28 mo during which individuals increase in weight from approximately 4 to 900 g. This represents an instantaneous growth rate of 0.645–0.785 $g \cdot d^{-1}$ which is consistent with that found for the landlocked form in laboratory studies conducted at 5–10°C. Applegate (1950) found an instantaneous growth rate of 0.890 $g \cdot d^{-1}$ for the landlocked sea lamprey in Lake Huron for the active feeding period of April through to December.

Some insight on the impact of the anadromous sea lamprey on their host species is possible from information collected at Mactaquac fishway on the St. John River. Examination of all Atlantic salmon captured in the fishway during the years 1972 to 1975 inclusive provided an opportunity to determine the incidence of scarring on this species. Personnel from Dep. Fisheries and Oceans examined salmon for length, sex, and the presence and location of marks including scars attributable to attack by sea lampreys. Fresh wounds were not differentiated from scars but were relatively scarce. No information was collected on scar size nor was it possible to estimate when the attack occurred.

The number of Atlantic salmon captured each year increased from 5876 to 18 391 between 1972 and 1975 (Table 5). Over this interval, the number of salmon bearing lamprey scars increased from 156 to 2817 equivalent to relative incidences of 2.6–15.0% (Table 5). The incidence of scarring from the St. John River is much higher than that recorded by Keenleyside (1956) for Atlantic salmon from the estuary (0.46%) and two salmon fences (0.14 and 0.15%) in the Miramichi River. Among the landlocked sea lampreys of the Great Lakes, Coble (1967) found scars on 10% of the large white suckers examined between 1947 and 1953. From 1953 to 1961, up to 40% of the large white suckers examined showed evidence of predation, the increase being coincident with the destruction of the lake trout population. Incidence of sea lamprey marks on fish from Lake Ontario varied widely from less than 1% for lake herring, *Coregonus artedii*, to over 35% for lake trout, *Salvelinus namaycush*, between 1954 and 1963 (Christie and Kolenosky 1980). Among coho, *Oncorhynchus kisutch*, and chinook salmon, *O. tshawytscha*, planted in Lake Ontario incidences of sea lamprey attack as high as 100% prior to lamprey control have been reported by Pearce et al. 1980. Scarring rates of whitefish, *Coregonus lavaretus*, in Loch Lomond, Scotland attributable to sea lampreys average approximately 45% (Maitland 1980).

It is presumed lampreys are attracted to their hosts principally by olfactory cues. In adult lampreys the olfactory organ is well developed with the epithelium of the nasal sac raised into numerous longitudinal folds which extend radially into the lumen of the nasal capsule forming a number of pockets (Kleerekoper 1972). Circulation of water in the nasal sac is facilitated by rhythmic respiratory contractions of the pharyngeal or branchial chamber which allows for a high efficiency of sampling of the environmental water. The positive correlation between relative incidence of scarring and number of migrating salmon suggests the cumulative release of chemical cues from a large concentration of fish is relatively more effective in attracting lampreys than that from a smaller group of individuals. In support of this suggestion a laboratory examination on the performance of a series of naturally produced chelating ligands in attracting juvenile landlocked sea lampreys indicated a critical threshold concentration for some chemicals below which behavior was not affected (F. W. H. Beamish unpublished data).

Migrant Atlantic salmon at the Mactaquac fishway fell into two distinct categories, grilse and salmon, the former representing fish returning after 1 yr at sea, the latter after 2 or more years in the ocean. Grilse ranged in length from 36 to 66 cm, the mode being approximately 55 cm. The length range of salmon was 66–102 cm with a modal value of 78 cm. On the basis of scarring incidence there was no significant difference ($P > 0.05$) in host preference for salmon over grilse in 1973 (Fig. 10). In 1972, 1974 and 1975 the incidence of scarring suggested a significant preference ($P < 0.05$) for salmon over grilse. In accord, a host size preference by the landlocked sea lamprey of the Great and Finger Lakes has been demonstrated for several teleosts including splake, *Salvelinus namaycush* × *S. fontinalis* (Berst and Spangler 1970), lake trout, *S. namaycush* (Wigley 1959; Budd et al. 1969; Farmer and Beamish 1973), rainbow trout, *Salmo gairdneri* (Berst and Wainio 1967), and carp, *Cyprinus carpio* (Farmer and Beamish 1973).

Scars occurred more frequently among female than

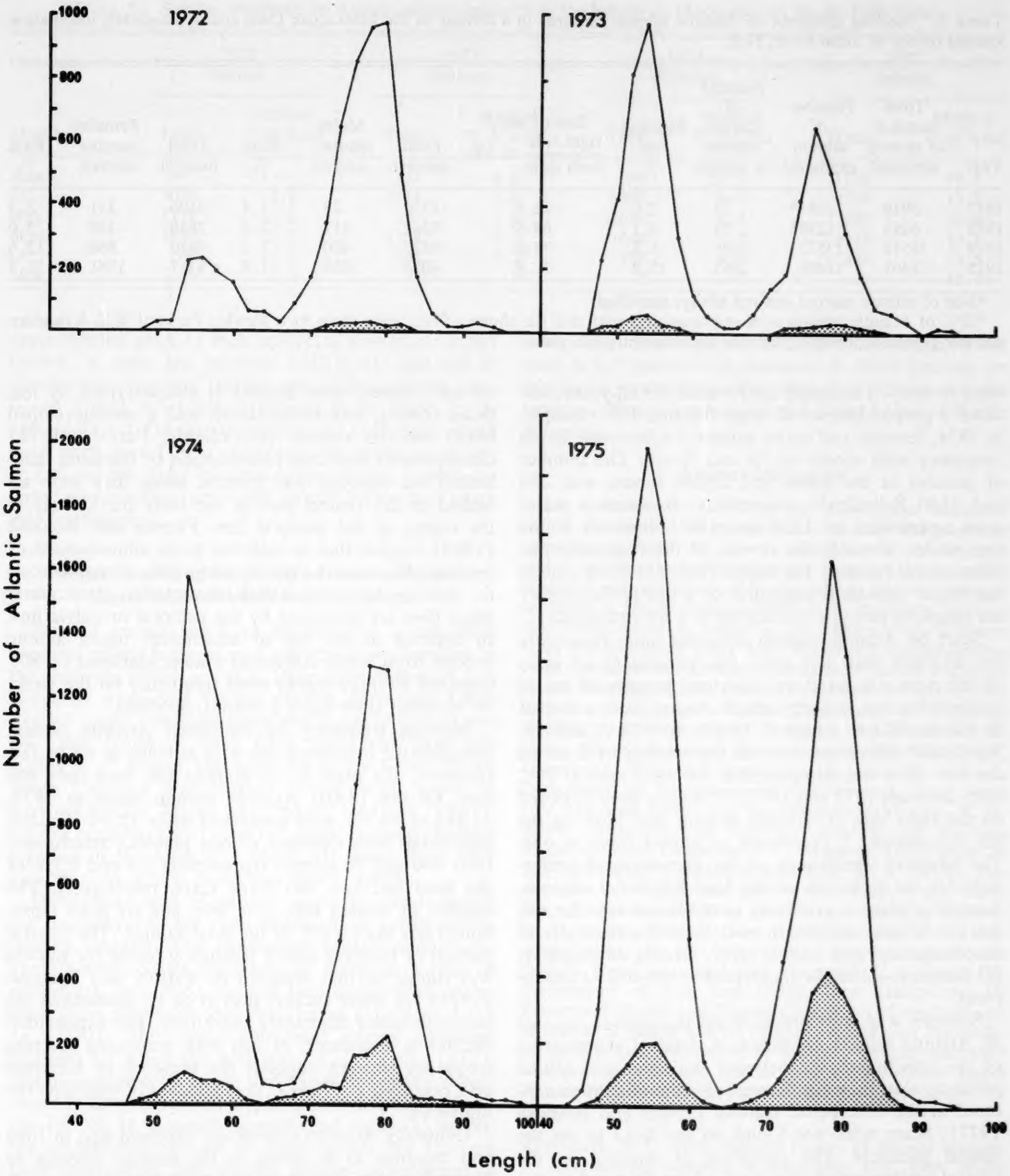

FIG. 10. Length–frequency distribution of Atlantic salmon captured at the fishway at the Mactaquac Dam on the St. John River, New Brunswick. The shaded area indicates the number of scarred salmon, the open area, the total number captured within each 2-cm length-class.

male Atlantic salmon. Relative rate of scarring for females increased from 3.19 to 18.90% between 1972 and 1975. The scarring rate for males was only slightly more than half that for females rising from 1.41 to 11.64% over the same time span (Table 5). The sex ratio of Atlantic salmon was for most years remarkably

TABLE 5. Scarring incidence on Atlantic salmon captured in a fishway at the Mactaquac Dam and hydroelectric installation located on the St. John River, N.B.

Year	Total number of salmon captured	Number of salmon examined	Number of scarred salmon in sample	Scarring rate %	Site of scar,[a] $\frac{\text{right side}}{\text{both sides}} \times 100$		Males			Females	
						Total number	number scarred	Rate %	Total number	number scarred	Rate %
1972	5919	1183[b]	31	2.6	72.3	1770	25	1.4	4106	131	3.2
1973	6195	1239[b]	51	4.1	63.6	3342	117	3.5	2848	143	5.0
1974	13573	13573	1186	8.7	76.6	6630	480	7.2	6830	860	12.6
1975	18401	18401	2765	15.0	71.4	9074	1056	11.6	9317	1761	18.9

[a] Side of salmon scarred was not always identified.

[b] 20% of Atlantic salmon were examined and analyzed, the choice of fish being made by a Hewlett Packard 9830 A random number generator incorporated into the data entry program.

close to unity. The length distribution for all years indicated a preponderance of large females. For example, in 1974, females and males exhibited a bimodal length frequency with modes of 54 and 78 cm. The number of females at the lower and higher modes was 230 and 1140 individuals, respectively. In contrast males were represented by 1330 and 100 individuals at the two modes, virtually the reverse of the frequency distribution for females. The higher rate of scarring among the longer females is suggestive of a size preference by sea lampreys perhaps in addition to a sex preference.

Scars on Atlantic salmon occurred more frequently on the right than left side. The percentage of scars on the right side relative to the total number of marks attributed to sea lamprey attack ranged from a low of 63.6% in 1973 to a high of 76.6% in 1974 (Table 5). Significant differences between the number of scars on the two sides was demonstrable for each year at $P < 0.05$. Between 1972 and 1975, 3156 scars were recorded on the right side of Atlantic salmon and 1205 on the left representing a preference of almost three to one. The adaptive significance of the demonstrated preference for the right side of the host fish is not obvious. Assuming bilateral symmetry in the blood vascular system of Atlantic salmon as well as in the thickness of the integument and muscle layer, feeding efficiency by sea lampreys should be unaffected by the side of attachment.

Scarring was most prevalent on the ventral areas of all Atlantic salmon examined. A detailed examination of the attachment site between the head and caudal peduncle was made for 50 scarred Atlantic salmon captured at the Mactaquac fishway (Potter and Beamish 1977). Scars were not found on the head or on the caudal peduncle. The incidence of scarring on the ventral surface represented 84% of the observed marks. This is remarkably similar to the scarring incidence of 83% recorded for the same region of landlocked Atlantic salmon in Maine (Davis 1967) and also parallels the distribution of scars on freshwater teleosts (Lennon 1954; Wigley 1959; Berst and Wainio 1967; and Farmer and Beamish 1973). The ventral areas of Atlantic salmon and indeed most teleosts is characterized by less dense scaling, thin musculature, and a well-developed blood vascular system. Accordingly, Farmer (1974) demonstrated that food consumption by the adult landlocked sea lamprey was greatest when they were attached to the ventral part of the body particularly in the region of the pectoral fins. Farmer and Beamish (1973) suggest that in addition to an enhancement of feeding efficiency it may be more difficult for teleosts to dislodge lampreys attached ventrally, particularly when they are protected by the pectoral or pelvic fins. In contrast to the site of attachment found among teleosts from North American waters, Maitland (1980) observed lamprey marks most frequently on the backs of whitefish from Loch Lomond, Scotland.

Scarring frequency on individual Atlantic salmon indicated the occasional fish with as many as six marks. However, the majority of marked fish bore only one scar. Of the 18 401 Atlantic salmon taken in 1975, 15 582 or 84.7% were unmarked while 12.5% or 2299 individuals bore evidence of one previous attachment. Only 436 and 56 salmon representing 2.4 and 0.3% of the total had two and three scars, respectively. The number of salmon with four, five, and six scars represented less than 0.2% of the total sample. The general pattern of multiple attack frequency found for salmon was similar to that reported by Farmer and Beamish (1973) for white suckers preyed on by landlocked sea lampreys under laboratory conditions. The exponential decline in abundance of fish with increasing scarring frequency strongly suggests the presence of lampreys on a host does not further the incidence of attack on the individual.

Generally Atlantic salmon are captured first in June and continue to be taken in the fishway through to November. Scarring incidence tended to decline with the progression of season (Table 6). In New Brunswick the spawning migration by sea lampreys is thought to begin as early as April. This would remove a significant proportion of feeding juveniles from the marine environment which subsequently may be reflected by lower scarring rates. Exactly when juvenile lampreys

TABLE 6. Scarring incidence on Atlantic salmon captured in the fishway at Mactaquac on the St. John River.

	1972 Salmon		1973 Salmon		1974 Salmon		1975 Salmon	
Month	Total	Marked % of total	Total	Marked % of total	Total	Marked % of total	Total	Marked % of total
June	—	—	187	4.8	550	27.3	1178	29.4
July	3030	2.8	3615	5.8	8850	8.7	9554	17.3
Aug.	1137	2.6	573	3.5	1610	6.2	1838	16.6
Sept.	1033	1.7	1158	0.2	1640	9.2	2915	13.3
Oct.	703	1.0	637	0.2	780	4.1	926	13.5
Nov.	16	0	25	0	0	0	33	18.2

cease feeding prior to their upstream movement is not known. A large sea lamprey (650 mm) captured in March approximately 160 km east of Nova Scotia contained a dark substance, presumed to be blood, in its intestinal tract. On the assumption this individual would have participated in a spawning migration some one or two months later it appears the marine trophic interval may continue until only shortly before their entry into freshwater.

Predation on and Mortality of Ammocoetes, Juvenile, and Adult Sea Lampreys

No fish species has been identified as a consistent predator of sea lamprey and reports of sea lamprey in the stomachs of fish are rare. In an examination of 514 swordfish stomachs, *Xiphias gladius*, Scott and Tibbo (1968) found a lamprey branchial basket in each of two fish. Sea lampreys have been recovered from the stomachs of striped bass captured in the Edisto River, South Carolina. Cannibalism among small adults in Barrows Stream, Maine was reported by Davis (1967). On one occasion Davis observed eight lampreys attached together in the form of a chain. Of these, three bore wounds from which blood was clearly visible.

Differential rates of natural mortality could explain the fluctuation in sex ratio observed for ammocoetes, feeding juveniles and nonfeeding upstream migrants. Female ammocoetes outnumbered males by a ratio of almost 2:1 ($n = 338$). Among feeding juveniles, males were more abundant than females at a ratio of 1:0.8 ($n = 220$). This trend continued among upstream migrants for which the ratio was 1♂ : 0.7♀ ($n = 456$). Not all ammocoetes which undergo transformation successfully complete metamorphosis and commence feeding (F. W. H. Beamish unpublished data). However, the distribution by sex of those which fail has not been determined. The slightly greater commitment to parental investment by the female sea lamprey requires a larger accumulation of energy stores preparatory to successful reproduction. The relative hunting and feeding efficiencies of the two sexes is unknown. Sex reversal is a possibility which could also explain the shift in sex ratio which occurs between the ammocoete and adult stage. The explanation for the fluctuation in sex ratio is not understood; however, it could provide an additional approach to the integrated concept of sea lamprey control employed in the Great Lakes of North America.

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APPLEGATE, V. C. 1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish 55: 1–237.

BEAMISH, F. W. H. 1979. Migration and spawning energetics of the anadromous sea lamprey, *Petromyzon marinus*. Environ. Biol. Fish. 4: 3–7.

BEAMISH, F. W. H., AND I. C. POTTER. 1975. The biology of the anadromous sea lamprey (*Petromyzon marinus*) in New Brunswick. J. Zool., Lond. 177: 57–72.

BEAMISH, F. W. H., I. C. POTTER, AND E. THOMAS. 1979. Proximate composition of the adult anadromous sea lamprey, *Petromyzon marinus*, in relation to feeding, migration and reproduction. J. Anim. Ecol. 48: 1–19.

BEAMISH, F. W. H., P. D. STRACHAN, AND E. THOMAS. 1978. Osmotic and ionic performance of the anadromous sea lamprey, *Petromyzon marinus*. Comp. Physiol. Biochem. 60A: 435–443.

BERST, A. H., AND G. R. SPANGLER. 1970. Lake Huron: effects of exploitation, itnroductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 877–887.

BERST, A. H., AND A. A. WAINIO. 1967. Lamprey parasitism of rainbow trout in southern Georgian Bay. J. Fish. Res. Board Can. 24: 2439–2548.

BIGELOW, H. B., AND W. C. SCHROEDER. 1948. Fishes of the western North Atlantic. 2. Cyclostomes. Mem. Sears Fdn. Mar. Res. 1: 29–58.

1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv. Fish. Bull. 53: 1–577.

BREDER, C. M. JR. 1923. Certain fishes from Sandy Hook Bay. Copeia 1923(114): 2–3.

1931. Fish notes for 1929 and 1930 from Sandy Hook Bay. Copeia 1931(2): 39–40.

BUDD, J. C., F. E. J. FRY, AND P. S. M. PEARLSTONE. 1969. Final observations on the survival of planted lake trout in South Bay, Lake Huron. J. Fish. Res. Board Can. 26: 2413–2424.

CHRISTIE, W. J., AND D. P. KOLENOSKY. 1980. Parasitic phase of the sea lamprey (*Petromyzon marinus*) in Lake Ontario. Can. J. Fish. Aquat. Sci. 37: 2021–2038.

CHURCHILL, W. S. 1945. The brook lamprey in the Brule River. Trans. Wisc. Acad. Sci. Arts Lett. 37: 337–346.

COBLE, D. W. 1967. White sucker population of South Bay, Lake Huron, and effects of the sea lamprey on it. J. Fish. Res. Board Can. 24: 2117–2136.

CONTRONEI, G. 1924a. Il fenomeno dell'accorciamento in rattorto alla maturita sessuale e alla senescenza dei Petromizonti. Atti Accad. naz Lincedi Rc. (5) 33: 530–534.

1924b. Sulla dimensioni raggiunte dal *Petromyzon fluviatilis* e sul fenomeno dell'accorciamenta. Atti Accad. naz. Lincei Rc. (5) 33: 282–285.

1926. Sulla biologia dei Petromizonti. 3. Il fenomeno dell'accorciamento nella maturita sessuale del *Petromyzon marinus*. Atti Acad. naz Lincei Rc. (6) 3: 37–40.

DAVIS, R. M. 1967. Parasitism by newly transformed anadromous sea lampreys on landlocked salmon and other fishes in a coastal Maine lake. Trans. Am. Fish. Soc. 96: 11–16.

EVERMANN, B. W., AND W. C. KENDALL. 1900. Check list of the fishes of Florida. U.S. Comm. Fish Fish. Rep. 25. 899: 48.

FARMER, G.J. 1974. Food consumption, growth and host preferences of the sea lamprey, *Petromyzon marinus* L. Ph.D. thesis, Univ. Guelph, Guelph, Ont.

FARMER, G. J., AND F. W. H. BEAMISH. 1973. Sea lamprey (*Petromyzon marinus*) predation of freshwater teleosts. J. Fish. Res. Board Can. 30: 601–605.

FARMER, G. J., F. W. H. BEAMISH, AND P. F. LETT. 1977. Influence of water temperature on the growth rate of the landlocked sea lamprey (*Petromyzon marinus*) and the associated rate of host mortality. J. Fish. Res. Board Can. 34: 1373–1378.

FRY, F. E. J. 1947. Effects of the environment on animal activity. Univ. Toronto Biol. No. 55; Publ. Ont. Fish. Res. Lab. No. 68.

HAEDRICH, R. C. 1977. A sea lamprey from the deep ocean. Copeia 4: 767–768.

HARDISTY, M. W. 1944. The life history and growth of the brook lamprey (*Lampetra planeri*). J. Anim. Ecol. 13: 110–122.

1960. Sex ratio of ammocoetes. Nature (Lond.) 186: 988–989.

1964. The fecundity of lampreys. Arch. Hydrobiol. 60: 340–357.

1965. Sex differentiation and gonadogenesis in lampreys. Part 2. The ammocoete gonads of the landlocked sea lamprey, *Petromyzon marinus*. J. Zool. 146: 346–387.

1969. Information on the growth of the ammocoete larvae of the anadromous sea lamprey, *Petromyzon marinus*, in British Columbia rivers. J. Zool. (Lond.) 159: 134–144.

1971. Gonadogenesis, sex differentiation and gametogenesis, p. 295–359. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1, Academic Press, London.

HARDISTY, M. W., AND I. C. POTTER. 1971. The behaviour, ecology and growth of larval lampreys, p. 85–125. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1, Academic Press, London.

HUBBS, C. L. 1925. The life cycle and growth of lampreys. Mich. Acad. Sci. Arts Lett. Pap. 4: 587–603.

HUBBS, C. L., AND I. C. POTTER. 1971. Distribution, phylogeny and taxonomy, p. 1–65. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1, Academic Press, London.

KEENLEYSIDE, M. G. A. 1956. Lampreys and lamprey scars on Miramichi salmon. Fish. Res. Board Can. Rep. Biol. Sta. St. Andrews 67: 149.

KLEEREKOPER, H. 1972. The sense organs, p. 373–404. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 2, Academic Press, London.

LANZING, W. J. R. 1959. Studies on the river lamprey (*Lampetra fluviatilis*) during its anadromous migration. Uitgeversmaatschappit Neelandia-Utrecht. 1959: 11–82.

LARSEN, L. O. 1973. Development in adult, freshwater river lampreys and its hormonal control. Starvation, sexual maturation and natural death. Copenhagen. 172 p.

LENNON, R. E. 1954. Feeding mechanisms of the sea lamprey and its effect on host fishes. Fish. Bull. U.S. 56: 247–293.

LOWE, D. R., F. W. H. BEAMISH, AND I. C. POTTER. 1973. Changes in the proximate body composition of the landlocked sea lamprey, *Petromyzon marinus* (L.) during larval life and metamorphosis. J. Fish. Biol. 5: 673–682.

MACDONALD, T. H. 1959. Estimates of length of larval life in three species of lampreys found in Great Britain. J. Anim. Ecol. 28: 293–298.

MAITLAND, P. S. 1980. Scarring of whitefish (*Coregonus lavaretus*) by European river lamprey (*Lampetra fluviatilis*) in Loch Lomond, Scotland. Can. J. Fish. Aquat. Sci. 37: 1981–1988.

MANSUETI, R. J. 1962. Distribution of small, newly metamorphosed sea lampreys, *Petromyzon marinus*, and their parasitism on menhaden, *Brevoortia tyrannus*, in mid-Chesapeake Bay during winter months. Chesapeake Sci. 3: 137–139.

MATHERS, J. S., AND F. W. H. BEAMISH. 1974. Changes in serum osmotic and ionic concentrations in landlocked *Petromyzon marinus*. Comp. Biochem. Physiol. 49A: 677–688.

MISLIN, H. 1941. Der Phasenwechsel des Rheinlachses *Salmo salar* unter besonderer Berucksichtigung des Ernahrungsapparates. Rev. Suisse Zool. 48 (Suppl.): 1–181.

MOORE, J. W., AND F. W. H. BEAMISH. 1973. The food of ammocoetes of *Petromyzon marinus* and *Lampetra lamottenii*. J. Fish. Res. Board Can. 30: 7–15.

MOORE, J. W., AND I. C. POTTER. 1976. Aspects of feeding and lipid deposition and utilization in the lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). J. Anim. Ecol. 45: 699–712.

NIKOL'SKII, G.V. 1963. The ecology of fishes(Translated from Russian by L. Birkett). Academic Press, London.

O'BOYLE, R. N., AND F. W. H. BEAMISH. 1977. Growth and intermediary metabolism of larval and metamorphosing stages of the landlocked sea lamprey, *Petromyzon marinus* L. Environ. Biol. Fish. 2: 102–120.

OOI, E. C., AND J. H. YOUSON. 1977. Morphogenesis and growth of the definitive opisthonephros during metamorphosia of anadromous sea lamprey, *Petromyzon marinus* L. J. Embryol. Exp. Morphol. 42: 219–235.

PEARCE, W. A., R. A. BRAEM, S. M. DUSTIN, AND J. J. TIBBLES. 1980. Sea lamprey (*Petromyzon marinus*) in the Lower Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1802–1810.

POTTER, I. C. 1980. Ecology of larval and metamorphosing lampreys. Can. J. Fish. Aquat. Sci. 37: 1641–1657.

POTTER, I. C., AND F. W. H. BEAMISH. 1975. Lethal temperatures in ammocoetes of four species of lampreys. Acta Zool. 56: 85–91.

1977. The freshwater biology of adult anadromous sea lampreys *Petromyzon marinus*. J. Zool., Lond. 181: 113–130.

POTTER, I. C., F. W. H. BEAMISH, AND H. JOHNSON. 1974. Sex ratios of adult sea lampreys (*Petromyzon marinus*) from a Lake Ontario tributary. J. Fish. Res. Board Can. 31: 122–124.

POTTER, I. C., G. M. WRIGHT, AND J. H. YOUSON. 1978. Metamorphosis in the anadromous sea lamprey, *Petromyzon marinus* L. Can. J. Zool. 56: 561–570.

SCOTT, W.B., AND S.N. TIBBO. 1968. Food and feeding habits of swordfish, *Xiphias gladius*, in the western North Atlantic. J. Fish. Res. Board Can. 25: 903–919.

SIMPSON, A. C. 1951. The fecundity of the plaice. Fish. Invest. Lond. (Ser. 2) 17: 1–27.

TAYLOR, B. J. R. 1965. The analysis of polymodal frequency distributions. J. Anim. Ecol. 34: 445–452.

VLADYKOV, V. D. 1936. Occurrence of three species of anadromous fishes on the Nova Scotian banks during 1935 and 1936. Copeia (1936) No. 3: 168.

1951. Fecundity of Quebec lampreys. Can. Fish. Cult. 10: 1–14.

1952. Distribution des lamproies (Petromyzonidae) dans la province de Québec. Nat. Can. 79: 85–120.

WIGLEY, R. K. 1959. Life history of the sea lamprey of Cayuga Lake, New York. Fish Bull. U.S. Fish. Wildl. Serv. 59: 559–617.

YOUSON, J. H., G. M. WRIGHT, AND E. C. OOI. 1977. The timing of changes in several internal organs during metamorphosis of anadromous larval lamprey, *Petromyzon marinus* L. Can. J. Zool. 55: 469–473.

Review of the Ecology of Lampreys in Northern Europe[1]

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MAITLAND, P. S. 1980. Review of the ecology of lampreys in northern Europe. Can. J. Fish. Aquat. Sci. 37: 1944–1952.

The general distributions of *Petromyzon marinus*, and *Lampetra fluviatilis* and *L. planeri* in Europe are similar and include much of the west and north, whereas *Lethenteron japonicum* occurs only in the north. The larvae of all four species occupy areas of shaded silt (optimum particle size: 180–380 μm) in parts of streams where current velocities are about 0.4 m/s. The gradients of streams in which they occur range from 1.9 to 5.7 m/km. Though differing in small details, the life cycles have much in common and spawning occurs usually in the spring or early summer. Both males and females spawn only once and die after reproduction. After hatching, the small larvae drift downstream to suitable silt beds. Larval life is variable and may last from 3 to 5 yr or even more. Larval metamorphosis and downstream migration occur during spring and summer and takes place mainly at night. The larvae of all species feed on fine particulate matter — mainly microorganisms and detritus. Adult *L. planeri* do not feed, but those of the three other species grow and mature in the sea where they are parasitic on a variety of marine and anadromous teleosts. There are considerable differences among the fecundities of the four species — related very much to the size of the adult females. Relatively few data are available on the population dynamics of any of the species.

Key words: lampreys, ecology, Europe

MAITLAND, P. S. 1980. Review of the ecology of lampreys in northern Europe. Can. J. Fish. Aquat. Sci. 37: 1944–1952.

Petromyzon marinus et *Lampetra fluviatilis* et *L. planeri* ont en général la même distribution en Europe, soit la majeure portion des régions occidentale et septentrionale, alors que *Lethenteron japonicum* ne se trouve que dans le nord. Les larves des quatres espèces occupent des régions de limon ombragé (grosseur optimale des particules : 180–380 μm) dans les secteurs des cours d'eau où la vitesse du courant est d'environ 0,4 m/s. Le gradient des cours d'eau dans lesquels elles se trouvent varie de 1,9 à 5,7 m/km. Le cycle biologique de ces espèces, bien que différent par certains petits détails, se ressemble beaucoup, et la ponte a lieu ordinairement au printemps ou au début de l'été. Mâles et femelles ne frayent qu'une fois et meurent ensuite. Après éclosion, les petites larves dérivent vers des lits de limon convenables en aval. La durée de la phase larvaire varie de 3 à 5 ans et même plus. La métamorphose et l'avalaison se produisent au printemps et en été, cette dernière principalement la nuit. Les larves de toutes les espèces se nourrissent de matière particulaire fine — surtout micro-organismes et détritus. Les adultes de *L. planeri* ne se nourrissent pas, mais ceux des trois autres espèces croissent et mûrissent en mer, où elles vivent en parasites sur une variété de téléostéens marins et anadromes. Les quatres espèces diffèrent considérablement sous le rapport de la fécondité, qui est étroitement liée à la taille des femelles adultes. On a relativement peu de données sur la dynamique de l'une ou l'autre de ces espèces.

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THIS review is concerned only with those species of lamprey which occur in northern Europe, i.e. that part of Europe (as defined by Maitland 1977) whose catchment drains mainly northwards to the Atlantic and Arctic oceans, the North, Baltic, and White seas. There are four such species: sea lamprey, *Petromyzon marinus*; arctic lamprey, *Lethenteron japonicum*; European river lamprey, *Lampetra fluviatilis*, and European brook lamprey, *Lampetra planeri*. Several other species of lamprey occur in Europe, but their distribution is predominantly central and southern, and mainly in rivers draining into the Adriatic, Black, and Caspian seas (Vladykov 1973; Vladykov and Kott 1979).

Though a number of brief accounts of the biology of lampreys in northern Europe have appeared in recent general texts (Maitland 1977; Wheeler 1969, 1978) there have been few reviews of the literature on their ecology for some considerable time other than

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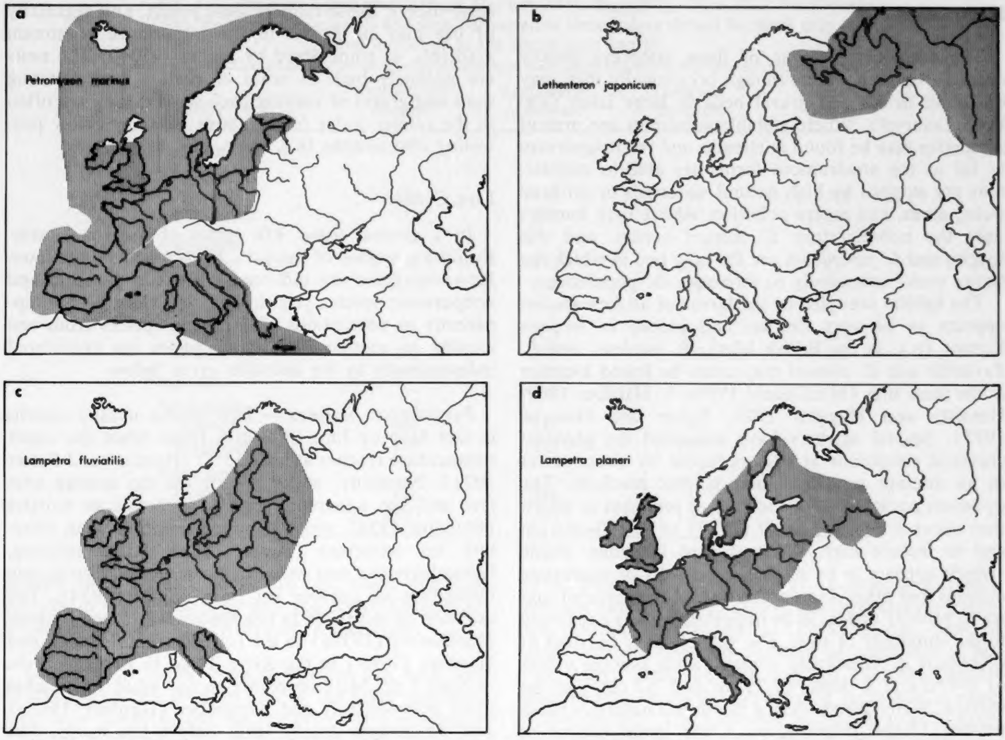

FIG. 1. European distribution of: (a) *Petromyzon marinus*, (b) *Lethenteron japonicum*, (c) *Lampetra fluviatilis*, (d) *Lampetra planeri*.

that by Hardisty and Potter (1971). An increasing amount of work has been (and is being) carried out by European ecologists, particularly in the British Isles, where Professor Hardisty and his co-workers have carried out a very valuable series of studies (Hardisty and Potter 1971). Since 1971 there has been considerable amount of work on the ecology of paired species of lampreys (Moore and Potter 1976; Bird and Potter 1979a, b). The present review embraces these and other work in northern Europe (Oliva 1953; Marinelli and Strenger 1954; Allegret et al. 1977) and gives a brief synthesis of what is currently known about the ecology of the four species named above.

DISTRIBUTION

Petromyzon marinus is a native anadromous species occurring over much of the Atlantic coastal area of western and northern Europe (from the White Sea area of western Russia (Konstantinov 1961) to the Mediterranean) and eastern North America (from Newfoundland to Florida), and in estuaries and easily accessible rivers there (Fig. 1). There are several landlocked populations in North America but for some reason none are found in Europe. *Lethenteron japonicum*, though also anadromous, occurs only in northern Europe, Asia, and western North America, in the sea and in river basins associated with the Arctic and Pacific oceans. There is practically no overlap of its distribution with those of the other three species (Fig. 1). *Lampetra fluviatilis* occurs over much of western and northern Europe from southern Norway to the western Mediterranean, where it is found in the sea and in accessible rivers. The species is mainly anadromous, but there are a few landlocked nonmigratory populations isolated from the sea (Abakumov 1959; Maitland 1972; Tuunainen et al. 1980). *Lampetra planeri* is a purely freshwater species occurring in streams and occasionally in lakes in northwest Europe, especially in basins associated with the North and Baltic seas. It has, however, also been recorded from western tributaries of the River Danube by Zanandrea (1959), Holcik (1970), and others (Blanc et al. 1971).

HABITAT

The ammocoete larvae of these lampreys usually occur in running waters though occasionally they may be found in silt and gravel beds in large lakes (e.g. Loch Lomond). Where suitable substrates are present all species may be found in streams and rivers upstream as far as the anadromous forms are able to migrate; they are stopped by high natural waterfalls or artificial weirs, dams, and severe pollution. Above such barriers only the nonmigratory *L. planeri* occurs, and this species and *L. japonicum* are the only two in which the larvae occur extensively in monospecific populations.

The habitat occupied by the larvae of all four species appears to be very similar, and indeed in western Europe (e.g. in the British Isles), *P. marinus*, and *L. fluviatilis* and *L. planeri* may often be found together at the same sites (MacDonald 1959a, b; Hardisty 1969; Hardisty and Huggins 1970; Potter and Osborne 1975). Several workers have measured the physicochemical conditions at sites occupied by ammocoetes in an attempt to define their habitat precisely. The optimum particle size of the beds of sediment in which they occur is said by Schroll (1959) to be 180–380 μm and to include clay, silt, and sand fractions. Shade (which appears to be related to growths of encrusting diatoms and other microorganisms on the surface) and water velocity appear to be important factors connected to the suitability of sites. The velocity over burrows of *L. planeri* is remarkably constant with average values of 0.4 m/s at a depth of 25 cm and 0.5 cm/s at the surface. Water speeds during floods are naturally much greater. Useful information on the larval habitat of *L. fluviatilis* in Finland is given by Kainua and Valtonen (1980).

Normally, suitable sites are found only in some parts of each river system. Baxter (1954, 1957) analyzed factors related to the distribution of lampreys in a number of British streams and found that most populations occurred where the average stream gradients were 1.9–5.7 m/km. Lampreys were rarely found where gradients exceeded 7.8 m/km. Within the stretches of suitable gradient, adequate sites are usually found in conditions of slowing current, where deposition of sand and silt occurs (e.g. in eddies, backwaters, behind obstructions, or at the edges of streams).

Relatively little is known about the precise habitats occupied by adult lampreys. Though adults of the parasitic species are sometimes caught at sea (Tambs-Lyche 1963), the precise conditions in which they occur have not been described. In freshwater, most adults are migrating upstream to spawn or are dying after spawning. Here, habitat seems only to be important in relation to their ability to swim upstream and the actual spawning sites selected — these appear to be similar for most species (Huggins and Thompson 1970). Hardisty (1961a) has noted that populations of *L. planeri* use the same sites for spawning for a number of years and that this is related to the physical characteristics of the streams at these points. This regularity of use may be linked to the importance of stream gradients, as emphasized by Baxter (1954). The nests are normally built in areas of shallow water among sand and gravel of varying particle size; they are often in the calmer water found above riffles or below protecting obstructions (e.g. weirs, bridges, etc.).

LIFE CYCLES

In a general sense, life cycles of the four north-European species of lamprey have much in common. However, there are differences between parasitic and nonparasitic species (e.g. in size, see Table 1) and apparently in populations of the same species from one locality to another. The four species are considered independently in the accounts given below.

Petromyzon marinus — This species usually spawns in late May or June in British rivers when the water temperature reaches at least 15°C (Hardisty and Potter 1971). Normally, males appear on the nesting sites first and are apparently highly attractive to females (Fontaine 1938), possibly by the secretion of an olfactory sex attractant (Sterba 1962). After hatching, larvae leave the nest and drift downstream, distributing themselves in suitable silt beds (Baxter 1954). The duration of larval life in this species was found by both MacDonald (1959a) in the Inler Burn in Scotland and Hardisty (1969) in the River Teme in England to be at least 5 yr. Metamorphosis to the adult form takes place between July and September (Hardisty 1961b) and the process usually takes only a few weeks. The time of the main downstream migration seems to vary from place to place, but in France was shown to occur invariably at night during December and January (Léger 1920). Relatively little is known about *P. marinus* in the sea and it appears to be found in both shallow, coastal, and deep offshore waters (Zanandrea 1962; Svetovidov and Ivanova-Berg 1970). Spawning migration in Europe takes place usually between April and June (Hardisty and Potter 1971) when the adults move upstream to reproduce.

Lethenteron japonicum — This species appears to spawn when the water temperature is about 12–15°C. The duration of the larval period has been estimated by Nikolskii (1956) as 3–4 yr. Metamorphosis in this northern species appears to take place early in the year — probably around May and June. Gritsenko (1968) found ammocoetes in the River Tymi in Siberia showing the first signs of metamorphosis in March and April. Downstream migration of the transforming adults takes place at night between late May and July: the species does not appear to feed during this migration (Gritsenko 1968). Nikolskii (1956) found that the length of adult life in the sea in the Sakhalin area was ~2 yr. The spawning migration of this species in the Bay of Sakhalin starts in August (Birman 1950),

TABLE 1. Comparative data on size (from Hardisty 1944; Berg 1948; Oliva 1953; MacDonald 1959a). Because of geographic and seasonal variation these values should be taken only as a general indication of the size of each species.

Feature	*Petromyzon marinus*	*Lethenteron japonicum*	*Lampetra fluviatilis*	*Lampetra planeri*
Length (mm)				
Ammocoete				
Average	129	167	120	144
Maximum	173	204	150	184
Adult male				
Average	781	475	315	121
Maximum	840	535	410	144
Adult female				
Average	773	505	330	124
Maximum	1200	575	420	151
Weight (g)				
Adult male				
Average	903	151	42	3
Maximum	910	228	104	5
Adult female				
Average	896	186	45	3
Maximum	2300	237	116	5

though Berg (1948) notes that the main migration periods in the River Vyg and the River Suchan are during September and December, respectively.

Lampetra fluviatilis — More research has been done in Europe on this than on any of the other European species of lamprey, and the life cycles of a number of different populations have been described. Spawning in British rivers starts when the water temperature reaches 10–11 °C, usually in March and April (Hardisty and Potter 1971), but further north it does not proceed until June (Berg 1948; Abakumov 1956). Nesting and spawning behavior have been described in some detail by Lauterborn (1926), Bahr (1953), and Hagelin (1959). After hatching, young larvae move out of the nest and redistribute themselves by drifting downstream and burrowing in suitable silt beds (Enequist 1937). The length of larval life has been estimated by a number of workers and has been variously put at 3 yr (Meek 1917; Hubbs 1925; Privolynev 1964), 4 yr (Hardisty and Huggins 1970), or 5 yr (Eglite 1958a; MacDonald 1959a). These differences are probably related to differences in latitude and other site factors (e.g. food, etc.). Metamorphosis usually takes place between July and September (Hardisty 1961b). The downstream migration appears to occur during darkness and its timing is highly variable, usually between March and June (Weissenberg 1925; Berg 1948; Zanandrea 1957). Macrophthalmia have recently been collected from power-station filters in the Firth of Forth in Scotland during this period. However, in the River Severn it can occur as early as late October, and as late as the following spring (Potter and Huggins 1973; Bird and Potter 1979a). *Lampetra fluviatilis* does not appear to feed during this downstream migration. Studies by Zanandrea (1959) in the Gulf of Gaeta indicate that the duration of adult life is just over 2.5 yr. Bahr (1952) suggests that this species tends to stay in coastal waters and especially in areas of low salinity. The spawning migration usually takes place between August and October, but its timing appears to vary widely from river to river (Tesch 1967) and a considerable body of information is available on this topic. The spawning migration is often initiated over a long period of time. Early migrants have been found in the Severn estuary between July and April, and the size of these migrants varies (Abou-Seedo and Potter 1979).

Lampetra planeri — The spawning season of this species in British rivers starts when water temperatures reach 10–11 °C — usually in March or April (Hardisty and Potter 1971). There is a clear relationship between water temperature and the numbers of animals observed at spawning sites, numbers declining as the temperature drops. The nest is normally an oval depression about 20–40 cm across and 2–10 cm deep (Loman 1912; Hardisty 1944; Lohnisky 1966). After hatching the young larvae leave the nest and distribute themselves by drifting further downstream and burrowing in suitable areas of silty sand (Baxter 1954; Thomas 1962). The duration of larval life has been estimated as 3 yr in Germany (Muller 1856; Lubosch 1903; Sterba 1953); 4 yr in Holland (Loman 1912), Finland (Ivanova-Berg 1931), Italy (Zanandrea 1953), Czechoslovakia (Balon 1957; Lohnisky 1966), and

TABLE 2. Comparative data on fecundity (from Berg 1948; Vladykov 1951; Hardisty 1964).

Feature	*Petromyzon marinus*	*Lethenteron japonicum*	*Lampetra fluviatilis*	*Lampetra planeri*
Eggs/female				
Average	172 000	94 000	16 000	1 550
Minimum	124 000	80 000	7 500	1 000
Maximum	260 000	107 000	28 000	2 000
Eggs/g body	204	505	373	440

Scotland (MacDonald 1959a); 5 yr in England (Hardisty 1961b) and Finland (Abakumov 1964); and 6 yr in England (Hardisty and Huggins 1970). Hardisty and Potter (1971) suggest that many of these values are underestimates and that in Great Britain at least the average duration of the larval period is 6.5 yr. Metamorphosis takes place between July and September (Zanandrea 1951; Hardisty 1961b; Malmquist 1978) usually simultaneously (i.e. within 3–4 wk) in any population (Hardisty et al. 1970). The adults probably do not move far after metamorphosis and continue to burrow like the ammocoetes. This behavior changes quite sharply when stream temperatures approach 10°C and the adults then migrate upstream for varying distances to their spawning grounds (Hardisty 1944; Malmquist 1980).

FOOD

Larvae — There is little evidence for any species-specific differences in food or feeding methods of the ammocoete larvae of the four species of north-European lamprey. All appear to feed from within their burrows on fine particulate matter, mainly microorganisms and in particular desmids and diatoms (Sterba 1953; Baxter 1954). Protozoa, including ciliates, euglenoids, and rhizopods, have also been found in ammocoete guts in some numbers. The role of detritus as food is uncertain, but Sterba (1962) found large amounts of it in ammocoete guts during the summer months. Moore and Potter (1975) have carried out a laboratory study of the feeding of the larvae of *L. planeri*. Most of the food taken in by larvae comes from the superficial sediments (including their microfauna) in the vicinity of their burrows.

The system of ciliated tracts in the pharynx, used as a means of transporting food on strands of mucus towards the intestine, has been described by Kiekebusch (1928), Newth (1930), and Sterba (1953, 1962). The notable observation by Mihail (1962) that ammocoetes can feed on large aquatic invertebrates and even trout fry has been supported recently by J. Jokiel (55 Powstancow Warszawy, 81 712 Sopot, Poland, personal communication). In view of the structure of the ammocoete mouth, however, it seems most unlikely that they would be able to ingest anything so large.

Adults — After metamorphosis, the adults of *L. planeri* do not feed at all and so need not be considered further here. The other three north-European species all feed as adults on fish in the sea, but detailed evidence of their feeding habits is rather fragmentary because of the difficulty of obtaining material. *Petromyzon marinus* apparently feeds on a wide variety of marine and anadromous fishes including sturgeon (*Acipenser sturio*), herring (*Clupea harengus*), shad (*Alosa alosa*), atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and atlantic salmon (*Salmo salar*). Salmon and sea trout *Salmo trutta* entering rivers on the east coast of Scotland often bear scars attributed to attacks by this species (Smith 1957): less frequently, *P. marinus* feeds on cetaceans (Van Utrecht 1959) such as *Phocoena phocoena*.

Lethenteron japonicum has been shown by Gritsenko (1968) to attack pink salmon (*Oncorhynchus gorbuscha*) and arctic char (*Salvelinus alpinus*) frequently, but small species such as smelt (*Osmerus eperlanus*) are also important hosts for this lamprey. Nikolskii (1956) found that 40% of smelt caught off the Sakhalin coast have marks resulting from attacks by this species. *Lampetra fluviatilis* is also known to feed on smelt, but its main prey species appear to be herring and sprat (*Sprattus sprattus*) (Bahr 1933; Eglite 1958a, b). Landlocked populations of *L. fluviatilis* are recorded as feeding mainly on whitefish *Coregonus lavaretus* (Robertson 1875; Maitland 1980), on smelt (Berg 1948), and on salmon (Abakumov 1959).

POPULATION DYNAMICS

Fecundity — Some early accounts of the eggs of lampreys are available (Yarrell 1831) and the numbers of eggs produced by the females in some populations of all the north-European species have now been estimated by various workers (Table 2). As might be expected, the largest numbers of eggs are found in *P. marinus* which produces an average of 172 000 eggs per female (Vladykov 1951). The greatest fecundity occurs in anadromous *P. marinus*. Of the smaller parasitic species *L. japonicum* produces some 94 000 eggs (Berg 1948) and *L. fluviatilis* about 16 000 per female (Hardisty 1964). The smallest and the only nonparasitic species, *L. planeri*, produces far fewer eggs, estimated by Hardisty (1964) at about 1500 per female.

Numbers — There are very few quantitative data available for the numbers or densities of larval lampreys in streams in northern Europe. However, because of their commercial importance there are considerable statistics relating to adult populations of larger anadromous species — the data usually concerned with the annual catches of the species concerned, rather than their total populations. Thus Abakumov (1956) records the catches of *L. fluviatilis* from the River Gauya between 1880 and 1912 as varying from 450 000 to almost 1 400 000 individuals. Similarly, Lanzing (1959) records catches of this species from the River Meuse between 1953 and 1957 as ranging from 95 000 to 200 000 individuals. The distribution in Europe of commercial fisheries for *L. fluviatilis* has been studied by Sterba (1962), who pointed out that there is a tendency for the catches to increase from the west to the east of the Baltic area. There are still several important fisheries in Finland (Valtonen 1980).

Regular population studies of *L. planeri* were carried out in a small stream in England by Hardisty (1961a), who found that there was a tendency for years of high and low abundance to alternate. The numbers of spawning adults in the stretch of stream studied from 1947 to 1960 varied from less than 60 to over 220. There appeared to be no direct correlation between the fluctuations and meteorological conditions, but Hardisty (1961a) suggested that the differential recruitment of age-classes in different years is a possible explanation.

Mortality — The few assessments that have been made of the mortality rates of the ammocoetes of north-European lampreys suggest that they are probably rather low and consistent throughout the larval period (Hardisty 1961b). Apart from the effect of fluctuating physical factors (Damas 1950), especially during the embryonic period, it is known that the larvae are eaten by eels *Anguilla anguilla* (Thomas 1962), threespined stickleback *Gasterosteus aculeatus* (Sterba 1962), and other species of fish as well as several different bird species (Sjoberg 1980). Losses may be particularly high during the migration from the nest to the ammocoete silt beds. A high mortality may also occur at metamorphosis, for Gritsenko (1968) has recorded large numbers of dead metamorphosing ammocoetes in various Siberian rivers. Only a few parasites have been recorded from lampreys (Moravec and Malmquist 1977) and nothing is known of their effect on the hosts.

There are few records of factors affecting the mortality of adult lampreys. In view of the large numbers taken in commercial fisheries, and the long-term and serious effects of pollution and various barriers to upstream migration, man must be considered as the most serious threat to populations.

Discussion

It is of some interest to compare the different ecological strategies evolved by these four species of lampreys in relation to their apparent success in northern Europe. *Lethenteron japonicum* virtually never coexists with any of the others and may therefore have sole occupancy of the "lamprey niche" east of northern Sweden. However, it is an extremely successful species in these northern rivers and it is relevant to note that two subspecies and a number of local forms are recognized by Berg (1948).

There is considerable overlap among the geographic distributions and ecological areas occupied by *P. marinus* and *L. fluviatilis* and *L. planeri*, and as noted above the ammocoetes of all three species may be found together in silt beds in streams. *Petromyzon marinus* is usually the least common species, both in these larval associations and as adults seen during migration. It may owe its survival and success to the large size of the adult which enables it to parasitize large host species in the sea and to be individually the most fecund of all lamprey species.

Lampetra planeri, however, is a very small species but because of this and the fact that its life cycle is completed entirely within running water, it is able to occupy small streams — often above obstructions which are difficult for the anadromous species to overcome during their upstream migrations. Thus in most river systems in northwest Europe, *L. planeri* is the most widespread species with isolated upstream populations able to recruit young continuously downstream to areas where they may have to compete with other lamprey species. *Lampetra planeri* is often the most common species even in these downstream associations.

Of the three west-European species, *L. fluviatilis* appears to be the most versatile, and in addition to having both anadromous and purely freshwater populations in some areas, a wide range of adult size is found in different populations. It is the most abundant migratory lamprey in west-European rivers.

There is considerable contrast between man's attitude to lampreys in northern Europe and in North America. In both areas these animals are of considerable economic importance, but in the former as a food source, in the latter as a serious pest of valuable freshwater commercial fisheries. In Europe, other than the exceptional series of studies by Hardisty, relatively little detailed ecological work has been carried out. The populations of migratory species have declined dramatically in some areas, mainly due to pollution and barriers in rivers, and in a number of rivers the populations of *P. marinus* and *L. fluviatilis* have disappeared. Some have recovered in recent years (Huddart and Arthur 1971), but many formerly successful fisheries have been discontinued. In North America, on the other hand, there has been in recent years intensive research on all aspects of the biology of lampreys (especially *P. marinus*) and a large body of information is now available covering both pure and applied aspects.

The contrast may be emphasized by two meetings recently attended by the author. One in Strasbourg, in December 1978, approved a Council of Europe paper promoting the conservation of freshwater fish in Europe. In this document, proposals for the conservation of lampreys, including *P. marinus*, were put forward: these included the maintenance of free access and special pollution control measures in some of the rivers in which populations are still present. A second meeting, the Sea Lamprey International Symposium in Marquette, Michigan, in August 1979, was convened mainly to assess the best means of eliminating *P. marinus* in the Great Lakes area of North America. The contrast in the problem on either side of the Atlantic is remarkable.

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ABAKUMOV, V. A. 1956. The mode of life of the Baltic river lamprey. Vop. Ikhtiol. 6: 122–128.

1959. The damage done by lampreys to fish stocks. Rybn. Khoz. 35: 32–33.

1964. On the systematics and ecology of the European brook lamprey *Lampetra planeri* (Bloch). Vop. Ikhtiol. 4: 423–432.

ABOU-SEEDO, F. S., AND I. C. POTTER. 1979. The estuarine phase in the spawning run of the river lamprey *Lampetra fluviatilis*. J. Zool. (Lond.) 188: 5–25.

ALLEGRET, P., C. DENIS, AND J. LE LANNIC. 1977. Obtention, au laboratoire de taux de croissance élevées chez les ammocètes de *Lampetra planeri* (Bloch) par une nouvelle méthode d'alimentation. Comparaison avec croissances naturelles. Ann. Hydrobiol. 17: 255–262.

BAHR, K. 1933. Das Flüssneunage (*Lampetra fluviatilis*) als Urheber von Fischveretzungen. Mitt. Dt. Seefisch Ver. 49: 1.

1952. Beiträge zur Biologie des Flüssneunauges, *Petromyzon fluviatilis* L. Zool. Jahrb. 81: 408–426.

1953. Beiträge zur Fortpflanzungsbiologie des Flüssneunauges *Petromyzon fluviatilis* L. Zool. Jahrb. 82: 58–69.

BALON, E. 1957. Contribution to the growth and biometry of larvae of the lamprey *Lampetra planeri* (Bloch, 1784) from the River Lucina in Silesia. Vest. Cesk. Spol. Zool. 21: 193–202.

BAXTER, E. W. 1954. Studies on the biology of lampreys. Ph.D thesis, University of London, London.

1957. Lamprey distribution in streams and rivers. Nature (London) 180: 1145.

BERG, L. S. 1948. Freshwater fishes of the U.S.S.R. and adjacent countries. (Transl. from Russian by the Israel Program for Scientific Translations, Jerusalem.)

BIRD, D. J., AND I. C. POTTER. 1979a. Metamorphosis in the paired species of lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). 1. A description of the timing and stages. Zool. J. Linn. Soc. Lond. 65: 127–143.

1979b. Metamorphosis in the paired species of lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). 2. Quantitative data for body proportions, weights, lengths and sex ratios. Zool. J. Linn. Soc. Lond. 65: 145–160.

BIRMAN, I. B. 1950. Parasitism of salmon of the genus *Oncorhynchus* by the Pacific lamprey. Izv. Inst. Ryb. Khoz. Okeonogr. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 290.)

BLANC, M., P. BANARESCU, J.-L., GAUDET, AND J.-C. HUREAU. 1971. European inland water fish. A multilingual catalogue. Fishing New (books) Ltd., London.

DAMAS, H. 1950. La ponte en aquarium des lamproies fluviatiles et de planer. Ann. Soc. Zool. Belg. 81: 151–162.

EGLITE, R. 1958a. The biology of the river lamprey in the Latvian SSR. Gidrobiol. Issled. Talinn. 1: 234–269.

1958b. The feeding havits of the river lamprey, *L. fluviatilis* (L.) in the sea. Zool. Zh. 37: 1509–1514.

ENEQUIST, P. 1937. Das Bachneunauge als ökologische Modification des Flüssneunauges. Uber die Flüssneunaugen und Bachneunaugen Schwedens. Ark. Zool. 29: 1–22.

FONTAINE, M. 1938. La lamproie marine. Sa pêche et son importance économique. Bull. Soc. Oceanogr. Fr. 17: 1681–1687.

GRITSENKO, O. F. 1968. K voprosu ob Ekologicheskoh parallelizne mezhdu minogami i posesyami. Izv. Inst. Ryb. Khoz. Okeanogr. 65: 157–169.

HAGELIN, L. O. 1959. Further aquarium observations on the spawing habits of the river lamprey (*Petromyzon fluviatilis*). Oikos 10: 50–64.

HARDISTY, M. W. 1944. The life history and growth of the brook lamprey (*Lampetra planeri*). J. Anim. Ecol. 13: 110–122.

1961a. Studies on an isolated spawning population of brook lamprey (*Lampetra planeri*). J. Anim. Ecol. 30: 339–355.

1961b. The growth of larval lampreys. J. Anim. Ecol. 30: 357–371.

1964. The fecundity of lampreys. Arch. Hydrobiol. 60: 340–357.

1969. Information on the growth of the ammocoete larvae of the anadromous sea lamprey *Petromyzon marinus* in British rivers. J. Zool. (Lond.) 159: 139–144.

HARDISTY, M. W., AND R. J. HUGGINS. 1970. Larval growth in the river lamprey *Lampetra fluviatilis* L. J. Zool., (Lond.) 161, 549–559.

HARDISTY, M. W., AND I. C. POTTER. 1971. The biology of lampreys, Volume 1. Academic Press, London.

HARDISTY, M. W., I. C. POTTER, AND R. STURGE. 1970. A comparison of the metamorphosing and macrophthalmia stages of the lampreys *Lampetra fluviatilis* and *Lampetra planeri*. J. Zool. (Lond.) 162: 383–400.

HOLČIK, J. 1970. Discovery of the brook lamprey — *Lampetra planeri* (Bloch, 1784) in the Hornád River (Danube Basin, Czechoslovakia). Vestn. Cesk Spol. Zool. 34: 304–308.

HUBBS, C. L. 1925. The life cycle and growth of lampreys. Pap. Mich. Acad. Sci. 4: 587–603.

HUDDART, R., AND D. R. ARTHUR. 1971. Lampreys and teleost fish other than whitebait in the polluted Thames estuary. Int. J. Environ. Stud. 2: 143–152.

HUGGINS, R. J., AND A. THOMPSON. 1970. Communal spawning of brook and river lampreys, *Lampetra planeri* Bloch and *Lampetra fluviatilis* L. J. Fish. Biol. 2: 53–54.

IVANOVA-BERG, M. M. 1931. Über die Lebensdauer der Larve von *Lampetra planeri* aus dem Finnischen Busens. Zool. Anz. 96: 330–334.

Kainua, K., and T. Valtonen. 1980. Distribution and abundance of European river lamprey (*Lampetra fluviatilis*) larvae in three rivers running into Bothnian Bay, Finland. Can. J. Fish. Aquat. Sci. 37: 1960–1966.

Kiekebusch, H. H. 1928. Bau und Entvicklung der Schildruse bei Neunaugenlarven (*Lampetra fluviatilis* L. und *Lampetra planeri* Bl.) Z. Morphol. Oekol. Tiere 11: 247–360.

Konstantinov, K. G. 1961. Sea lamprey (*Petromyzon marinus* L.) off the Murman shore. Zool. Zh. 40: 938–939.

Lanzing, W. J. R. 1959. Studies on the river lamprey *Lampetra fluviatilis* during its anadromous migration. Uitsgever. Neerlandia, Utrecht.

Lauterborn, R. 1926. Das Laichen des Flüssneunauges (*Lampetra fluviatilis* L.) in den Seitengewässern des Oberrheins. Zool. Anz. 8(5/6).

Léger, M. L. 1920. Jeunes studes d'eau douce et biologie de la lamproie marine. C. R. Acad. Sci. 179: 251–255.

Lohnisky, K. 1966. The spawning behaviour of the brook lamprey, *Lampetra planeri*. Vestn. Cesk. Spol. Zool. 30: 289–307.

Loman, J. C. C. 1912. Über die Naturgeschichte des Bachneunauges *Lampetra planeri*. Zool. Jahrb. 15: 243–270.

Lubosch, W. 1903. Über die Geschlechts differenzierung bei Ammocoetes Verh. Anat. Ges. Jena 17: 66–74.

MacDonald, T. H. 1959a. Estimates of length of larval life in three species of lamprey found in Britain. J. Anim. Ecol. 28: 293–298.

1959b. Identification of ammocoetes of British lampreys. Glasg. Nat. 18: 91–95.

Maitland, P. S. 1972. Loch Lomond: Man's effects on the salmonid community. J. Fish. Res. Board Can. 29: 849–860.

1977. Freshwater fishes of Britain and Europe. Hamlyn, London.

1980. Scarring of whitefish (*Coregonus lavaretus*) by European river lamprey (*Lampetra fluviatilis*) in Loch Lomond, Scotland. Can. J. Fish. Aquat. Sci. 37: 1981–1988.

Malmquist, B. 1978. Population structure and biometry of *Lampetra planeri* (Bloch) from three different watersheds in South Sweden. Arch. Hydrobiol. 84: 65–86.

1980. The spawning migration of the brook lamprey, *Lampetra planeri* Bloch, in a south Swedish stream. J. Fish. Biol. 16: 105–114.

Marinelli, W., and A. Strenger. 1954. *Lampetra fluviatilis* (L.) *In* Vergleichende Anatomie und Morphologie der Wilbeltiere. I. Lieferung. Franz Deuticke, Wien.

Meek, A. 1917. The lampreys of the Tyne. Rep. Dove Mar. Lab. 6: 49–51.

Mihail, N. 1962. Zur Biologie und Ökologie von *Eudontomyzon danfordi*. Zool. Anz. 168: 139–143.

Moore, J. W., and I. C. Potter. 1975. A laboratory study on the feeding of the larvae of the brook lamprey *Lampetra planeri* (Bloch). J. Anim. Ecol. 45: 81–90.

1976. Aspects of feeding and lipid deposition and utilisation in the lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). J. Anim. Ecol. 45: 699–712.

Moravec, F., and B. Malmquist. 1977. Records of *Cucullanus truttae* (Fabricius 1794) (Nematoda, Cucullanidae) from Swedish brook lampreys, *Lampetra planeri* (Bloch). Folia. Parasit. (Praha) 24: 323–329.

Muller, A. 1856. On the development of the lampreys. Ann. Mag. Nat. Hist. 18: 298–301.

Newth, H. G. 1930. The feeding of ammocoetes. Nature (London) 126: 94–95.

Nikolskii, G. V. 1956. Some data on *Lampetra japonica* (Martens) during the period of sea life. Zool. Zh. 35: 589–591.

Oliva, O. 1953. A contribution to the review of native lampreys (Petromyzones Berg 1940). Vestn. Kral. Cesk. Spol. Nauk. Tr. Mat.-Prirodoved. 9: 1–19.

Potter, I. C., and R. J. Huggins. 1973. Observations on the morphology, behaviour and salinity tolerance of downstream migrating river lampreys (*Lampetra fluviatilis*). J. Zool. (Lond.) 169: 365–379.

Potter, I. C., and T. S. Osborne. 1975. The systematics of British larval lampreys. J. Zool. (Lond.) 176: 311–329.

Privolnyev, 1964. Ecological and physical features of the larval river lamprey *Lampetra fluviatilis* (L.). Izv. Inst. Ozern. Rechn. Ryb. Khoz. 58: 180–185.

Robertson, D. 1875. On *Petromyzon fluviatilis* and its mode of preying on *Coregonus clupeoides*. Trans. Nat. Hist. Soc. Glasg. 2: 61–62.

Schroll, F. 1959. Zur Ernahrungsbiologie der steirischen Ammocoten *Lampetra planeri* (Bloch) unde *Eudontomyzon danfordi* (Regan). Int. Rev. Ges-amten Hydrobiol. 44: 395–429.

Sjöberg, K. 1980. Ecology of the European river lamprey (*Lampetra fluviatilis*) in northern Sweden. Can. J. Fish. Aquat. Sci. 37: 1974–1980.

Smith, I. W. 1957. The occurrence of damaged sea trout on the east coast of Scotland. Salmon Trout Mag. (London) 1957: 148–150.

Sterba, G. 1953. Die Physiologie und Histogenese der Schilddruse und der Thymus beim Bachneunauge (*Lampetra planeri* Bloch - *Petromyzon planeri* Bloch). Wiss. Z. Fr. Schiller-Univ. Jena 2: 239–298.

1962. Die Neunaugen (Petromyzonidae). Hanbd. Binnenfisch. Mitteleurop. 3: 263–352.

Svetovidov, A. N., and M. M. Ivanova-Berg. 1970. New records of the marine lamprey (*Petromyzon marinus*) from the Gulfs of Riga and Finland. Zool. Zh. XLIX: 160–161.

Tambs-Lyche, H. 1963. Norwegian Petromyzontidae. Sarsia 11: 21–24.

Tesch, W. F. 1967. Aktivität und Verhälten wandernder *Lampetra fluviatilis*, *Lota lota* und *Anguilla* im Tidegebiet der Elbe. Helg. Wiss. Meeresunt. 16: 92–111.

Thomas, J. D. 1962. The food and growth of brown trout (*Salmo trutta* L.) and its feeding relationship with the salmon parr (*Salmo salar* L.) and the eel (*Anguilla anguilla* L.) in the River Teifi, West Wales. J. Anim. Ecol. 31: 175–205.

Tuunainen, P., E. Ikonen, and H. Auvinen. 1980. Lampreys and lamprey fisheries in Finland. Can. J. Fish. Aquat. Sci. 37: 1953–1959.

Valtonen, T. 1980. European river lamprey (*Lampetra fluviatilis*) fishing and lamprey populations in some rivers running into Bothnian Bay, Finland. Can. J. Fish. Aquat. Sci. 37: 1967–1973.

van Utrecht, W. L. 1959. Wounds and scars in the skin of the common porpoise, *Phocaena phocaena* (L.) Mammalia XXIII (1): 100–122.

Vladykov, V. 1951. Fecundity of Quebec lampreys. Can. Fish Cult. 10: 1–14.

1973. Petromyzonidae, p. 1–5. *In* Check-list of the fishes of the north-eastern Atlantic and of the Mediterranean. Clofnam, Paris.

Vladykov, V. D., and E. Kott. 1979. List of northern hemisphere lampreys (Petromyzonidae) and their distribution. Fish. Mar. Serv. Misc. Spec. Publ. 42: 30 p.

Weissenberg, R. 1925. Flüss — und Bachneunage (*Lampetra* *fluviatilis* L. und *Lampetra planeri* Bloch), ein morphologisch-biologischer Vergleich. Zool. Anz. 63: 293–306.

WHEELER, A. 1969. The fishes of the British Isles and North-West Europe. Macmillan, London, XVII: 613 p.

1978. Key to the fishes of northern Europe. Warne, London.

YARRELL, W. 1831. Remarks on the eggs and spawning-season of *Petromyzon fluviatilis* and *P. marinus*. Proc. Zool. Soc. Lond. 1: 133–134.

ZANANDREA, G. 1951. Rilieva è confronti biometrici et biologici sul *Petromyzon* (Lampetra) *planeri* Bloch. Boll. Pesca Piscic. Idrobiol. 6: 53–78.

1953. Note sulla ecologia è distribuzione in Italia della Lampreda di ruscello (*Lampetra planeri* Bloch). Boll. Pesca Piscic. Idrobiol. 8: 252–272.

1957. Esame critico è comparativo delle lamprede catturate in Italia. Arch. Zool. Ital. 42: 249–307.

1959. Lamprede parassite è non-parassite rel bacino del Danubio. Arch. Zool. Ital. 44: 215–249.

1962. Rapporti tra l'alto è il medio versante adriatico d'Italia nella biogeographia delle lamprede. Boll. Zool. 29: 727–734.

Lampreys and Lamprey Fisheries in Finland[1]

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TUUNAINEN, P., E. IKONEN, AND H. AUVINEN. 1980. Lampreys and lamprey fisheries in Finland. Can. J. Fish. Aquat. Sci. 37: 1953–1959.

There are three lamprey species in Finland. European river lamprey (*Lampetra fluviatilis*) is common along the coast of Finland and 28 rivers are known to support spawning populations while landlocked river lamprey populations exist in three watercourses. European brook lamprey (*Lampetra planeri*) is common in freshwater all over the country, and sea lamprey (*Petromyzon marinus*) has been reported off the Finnish coast only 19 times since 1854. Food of the river lamprey and landlocked river lamprey includes valuable fish species such as herring, sprat, and vendace, but no effects on the fish stocks have been reported. River lamprey catch in Finnish coastal rivers make up about 2–2.5 million individuals (100 t) and lampreys are used only for human consumption. The fishing season begins in August and ends in February. Environmental changes in rivers (dams, pollution, etc.) have caused great damage to river lamprey populations. Successful attempts have been made to promote spawning by transporting lampreys over the dams. Landlocked river lamprey, brook lamprey, and sea lamprey are of no economic significance in Finland.

Key words: sea lamprey, river lamprey, brook lamprey, distribution, Finland, life history, fisheries, management

TUUNAINEN, P., E. IKONEN, AND H. AUVINEN. 1980. Lampreys and lamprey fisheries in Finland. Can. J. Fish. Aquat. Sci. 37: 1953–1959.

Il y a trois espèces de lamproies en Finlande : la lamproie fluviatile européenne (*Lampetra fluviatilis*) est commune le long de la côte finlandaise, et l'on connaît 28 rivières qui supportent des populations reproductrices. Il existe des populations de lamproies fluviatiles cantonnées en eau douce dans trois cours d'eau. La lamproie de ruisseau européenne (*Lampetra planeri*) est commune en eau douce dans tout le pays. La grande lamproie marine (*Petromyzon marinus*) a été signalée au large de la côte finlandaise (seulement 19 fois depuis 1854). La nourriture de la lamproie fluviatile et de la même espèce cantonnée en eau douce comprend des espèces de poissons de valeur, tels le hareng, le sprat et le corégone blanc, sans qu'on ait signalé d'effets sur les stocks de poissons. Les prises de lamproie fluviatile dans les rivières côtières de la Finlande sont d'environ 2–2,5 millions de sujets (100 t). Elle ne sert qu'à la consommation humaine. La saison de pêche débute en août et se termine en février. Des pertubations environnementales dans les rivières (barrages, pollution, etc.) ont causé des dommages considérables aux populations de lamproies fluviatiles. On a réussi à promouvoir la reproduction en transportant des lamproies par-dessus les barrages. La lamproie fluviatile cantonnée en eau douce, la lamproie de ruisseau et la grande lamproie marine n'ont-aucune importance économique en Finlande.

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LAMPREYS are an important source of income for many fishermen along the coasts of Finland. However, lampreys have not been studied much in Finland and there have been only a few papers on lamprey taxonomy (Koli 1963, 1969, 1975), ecology (Wigren 1954, 1964; Tuikkala 1971; Valtonen and Tossavainen 1978), and fisheries (Hurme 1966; Tuikkala 1971, 1974; Storå 1978).

This paper is a review of the facts of lamprey biology and fisheries in Finland. The effects of changes in environment and lamprey management are also discussed.

LAMPREY SPECIES AND THEIR DISTRIBUTION

There are three species of lamprey in Finland: sea lamprey (*Petromyzon marinus*), European river lamprey (*Lampetra fluviatilis*), and European brook lamprey (*Lampetra planeri*).

Sea lampreys are found only occasionally off the coast of Finland and all sea lampreys captured in Finland have been single specimens. Since 1854, the Zoological Museum of the University of Helsinki has catalogued only 19 observations of this species mainly along the south coast.

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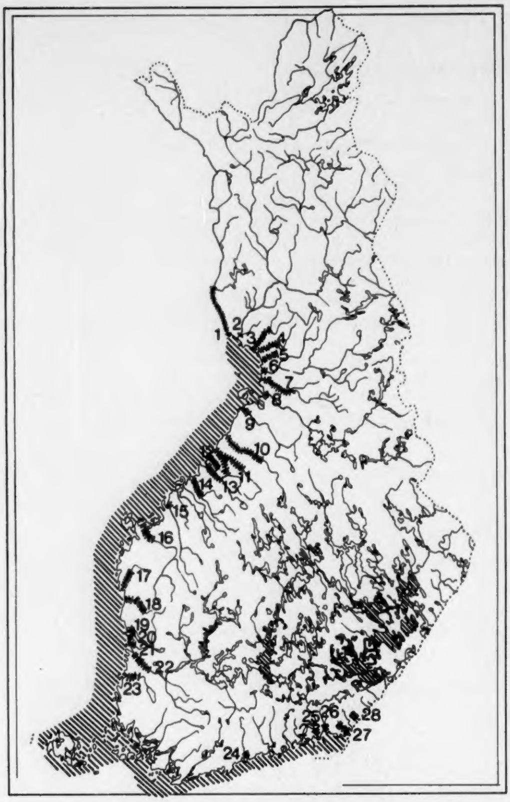

FIG. 1. Distribution of river lamprey in Finland. River lampreys are common along the coast. Lamprey fishing exists in many coastal rivers (shaded area), and lamprey stocks may also exist in rivers which are not indicated here. 1, Tornionjoki; 2, Kemijoki; 3, Simojoki; 4, Kuivajoki; 5, Olhavanjoki; 6, Iijoki; 7, Kiiminginjoki; 8, Oulujoki; 9, Siikajoki; 10, Pyhäjoki; 11, Kalajoki; 12, Siiponjoki; 13, Lestijoki; 14, Perhojoki; 15, Lapuanjoki; 16, Kyrönjoki; 17, Teuvanjoki; 18, Isojoki; 19, Merikarvianjoki; 20, Pohjajoki; 21, Eteläjoki; 22, Kokemäenjoki; 23, Eurajoki; 24, Vantaanjoki; 25, Kymijoki; 26, Summajoki; 27, Virojoki; 28, Urpalanjoki.

River lampreys are common along the entire coast of Finland. Formerly, most Finnish rivers flowing to the Baltic Sea supported river lamprey stocks, but because of changes in the natural state of the rivers (e.g. because of dams, pollution, etc.) many stocks have been destroyed or weakened (Fig. 1).

According to L. Koli (Zoological Museum of the University of Helsinki, 1979, personal communication), populations of landlocked river lampreys exist in the large lakes of the watercourses of the rivers Vuoksi, Kymijoki, and Kokemäenjoki (Fig. 1).

Brook lampreys exist in freshwater all over the country. Only to the north in the watershed of Maanselkä and in the Koutajoki River system, waters flowing to the Barents Sea and White Sea, respectively (Koli 1975), are no brook lamprey populations known.

LIFE HISTORY OF RIVER LAMPREYS IN FINLAND

Adult phase — Almost all that is known about the feeding migration of river lampreys in the Baltic is based on the observations of fishermen. According to these observations, lampreys are pelagic. Fishermen catching salmon by drift lines report that lampreys are often found attached to bait herring (*Clupea harengus*) or sprat (*Clupea sprattus*) and that, especially in summer, lampreys eat almost all of the herring, causing cessation of drift-line fishing.

Lampreys are caught by trawlers fishing for herring and sprat in the pelagic zone. Lampreys are also caught by trap nets in May and June. These trap nets are used for fishing for herring in depths of 5–20 m. Fishermen catching herring by gill nets at depths of 4–10 m have also found lampreys attached to herring. Lampreys found on drift-line baits have usually been smaller than lampreys found in trap nets or gill nets.

Lamprey scars have been found on herring and Atlantic cod (*Gadus morhua*) off the Finnish coasts. No Atlantic salmon (*Salmo salar*), sea trout (*Salmo trutta trutta*), or whitefish (*Coregonus lavaretus* s.l.) with lamprey scars have been reported. At the beginning of the spawning migration in August and September river lampreys stop feeding (Tuikkala 1971).

Scars attributed to landlocked river lampreys have been reported on vendace (*Coregonus albula*), pikeperch (*Stizostedion lucioperca*), and whitefish. In Lake Ladoga the landlocked river lampreys feed on smelt (*Osmerus eperlanus*) (Berg 1948) and salmon (Abakumov 1960).

The spawning run into the rivers begins in August. In the Bothnian Bay in the Pyhäjoki River, first captures take place in August and catches in this month have usually been about 5% of the total annual catch. The largest catches are taken in September and October and the fishing season ends in February. Observations of later spawning runs have been made: in the River Vantaa in the Gulf of Finland lampreys migrate into the river in May (L. Koli personal communication); a spring run also occurs in the Neva (Ivanova-Berg 1936; Berg 1948).

The homing behavior of river lampreys was studied in the Bothnian Bay by tagging experiments in September 1974. Lampreys were captured during the spawning migration at the river mouths of the Pyhäjoki and Kalajoki rivers (Fig. 2) and were tagged with Carlin tags. According to the results, river lampreys do not have a marked homing behavior. However, it is difficult to make definitive conclusions because lampreys were captured for tagging in rivers after reaching freshwater. This might have caused these lampreys to

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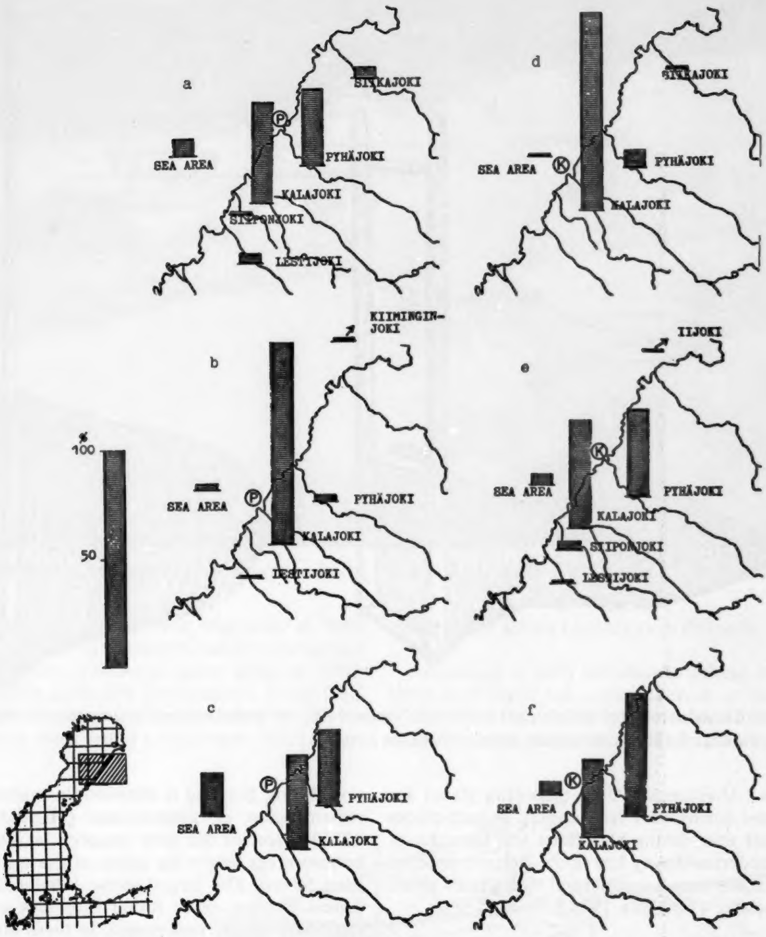
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FIG. 2. Results of river lamprey tagging experiments in Bothnian Bay in September 1974. Ⓚ indicates releasing places of lampreys captured in the mouth of the Kalajoki River and Ⓟ indicates releasing places of lampreys captured in the mouth of the Pyhäjoki River. (a) Number released (n) = 149, recaputre rate (p) = 65.8%; (b) n = 149, p = 69.8; (c) n = 150, p = 73.7; (d) n = 147, p = 88.4; (e) n = 148, p = 68.2; (f) n = 109, p = 57.8. Histograms show the recaptures in different areas as percentages of the total recaptures which occurred by March 1975.

lose their ability to rediscover their home river. It is also possible that surface currents in the Gulf of Bothnia were stronger than usual because of the southwest winds during the release period. This might have caused the water of the Kalajoki River to reach further north than usual resulting in a stronger attraction for lampreys. Similar results have been obtained in the Gulf of Riga (Abakumov 1956).

The distances from the sea of the uppermost spawning areas are known for some rivers. These are based on the situation of the uppermost fishing places. In many rivers the spawning run is obstructed by dams and other physical, as well as chemical, barriers. Spawning of river lampreys in Finnish rivers takes place at water temperatures of 12–14°C, usually in late May or early June (Tuikkala 1971), as also in rivers of the

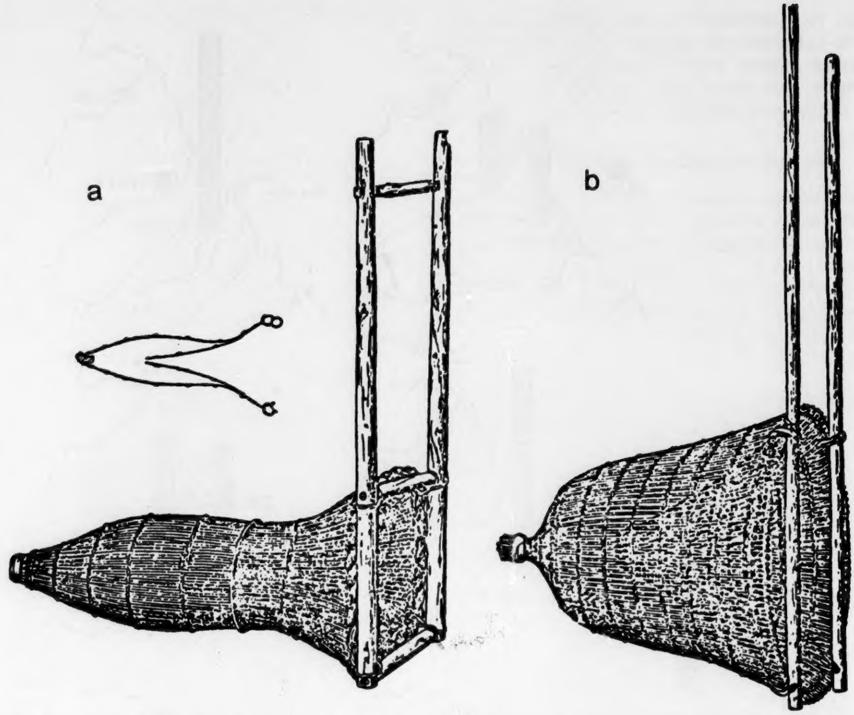

FIG. 3. Types of wooden lamprey baskets used in Finland (Sirelius 1908). (a) Basket made of willow used in the Bothnian Bay area; (b) basket made of willow used on the other parts of the coast.

Gulf of Riga (Abakumov 1956). Spawning places are usually situated downstream from rapids. In such places strong currents exist during high flows and the velocity of water is moderate during low flows. Bottom material in spawning areas is well-sorted sand with grains about 1 mm in diameter (Tuikkala 1971).

Eggs and larvae — After spawning, water temperatures rise to 13–18°C in about 2 wk. Before hatching, the eggs are found buried in the bottom sand and are subject to predation by insect larvae. Because of the scarcity of suitable spawning places, egg densities can be high and are estimated to be many thousands per square metre in some places (Tuikkala 1971). Larvae hatch 10–14 d after fertilization of the eggs, and they stay near the spawning area. The size of larvae at hatching is less than 10 mm (Tuikkala 1971). Tuikkala (1971) has found small larvae (8–36 mm) in densities of 40–2000 individuals/m^2 in the spawning areas. The larvae spend their first summer near these areas, burrowing in the sand. In their second summer they seem to move to finer bottom sediments containing high amounts of organic matter. Passive downstream migration during flooding is obviously a major factor in the redistribution of ammocoetes (Hardisty and Potter 1971). Most of the river lamprey larvae are found in bottom areas where the depth of the water is not more than 50 cm. The larger larvae inhabit slowly running waters but are never found in places where water is stationary all the year round. In these places the depth of bottom sediments varies from a few to about 100 mm (Tuikkala 1971).

Larvae spend 4–6 yr in the rivers before moving downstream to the sea; the duration of the larval phase increases from south to north (Koli 1975). Metamorphosis of larvae takes place at the end of their last summer spent in the river. After metamorphosis they feed on bottom animals, eggs of different fish species, and dead and living fishes (Tuikkala 1971).

Downstream migration takes place in spring during the night. River lampreys of about 120 mm moving to the sea in May have been captured by sampling gear developed for capturing downstream migrating whitefish larvae.

River lamprey larvae are subjected to predation by fish like burbot (*Lota lota*) and perch (*Perca fluviatilis*)

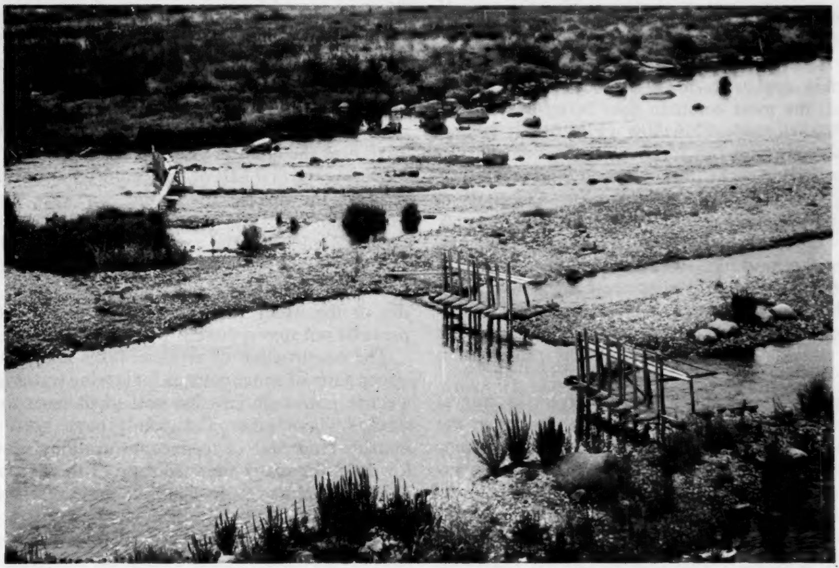

FIG. 4. Lamprey fishing by baskets set along trestles in the Kalajoki River in the Bothnian Bay in September 1978.

in rivers. During the downstream migration of lampreys, many fishermen have reported terns (*Sterna* sp.) feeding on lampreys. Lampreys never seem to occur in the diet of fishes in the sea. For instance, in the Gulf of Finland, 123 salmon stomachs were studied and no signs of lampreys were found (Andersson 1980).

FISHING FOR RIVER LAMPREYS IN FINLAND

According to early documents, fishing for river lampreys in Finland has occurred from at least the early 1500s. Even catch statistics are available for these early times, because lampreys were a taxable commodity.

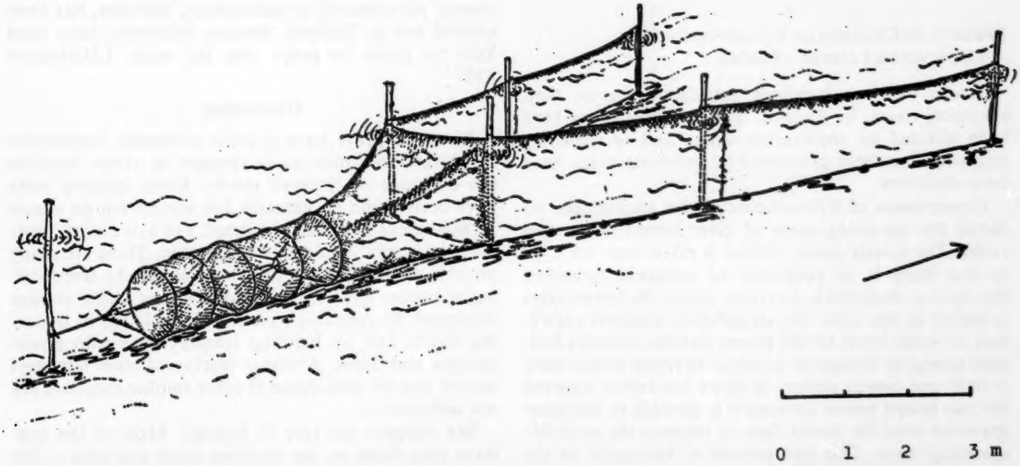

FIG. 5. Lamprey trap net set out for fishing. This gear has become more common lately. The arrow indicates the direction of current.

Storå (1978) has published a complete review of the history of lamprey fishing in the rivers of the Gulf of Bothnia.

Two main appliances are used for lamprey fishing in Finland, the most common gear being the wooden lamprey basket made of willow (Fig. 3). It is used during the spawning run in rivers. Individual baskets are set out among rocks in rapids with other rocks acting as weights. The other way of using baskets is to build trestles into the river along which the baskets are set (Fig. 4). The baskets are set out in the evening and checked in the morning. In full moonlight the baskets are not set out because catches are known to be very poor at that time (Tuikkala 1971; Storå 1978). Nowadays, also a second appliance, the lamprey trap net (Fig. 5) is widely used, usually in the mouth of a river near sea level.

Lamprey fishing usually begins in rivers in August when lampreys start their spawning run. However, the best catches are taken in September and October. Commercial fishing ceases at the beginning of November. In December, January, and February, only a few fishermen catch lampreys for consumption in their own households.

The total lamprey catch in Finland at the beginning of the 1970s was about 2.7–3.0 million individuals, which is about 130 t. The present catch is estimated to be about 2.0–2.5 million individuals (100 t) and fishing exists nowadays in 28 rivers (Fig. 1). Sea lampreys, landlocked river lampreys, and brook lampreys are not fished for in Finland.

The market price of river lampreys was 0.55 Fmk/individual (0.13 US $/individual) to fishermen in 1978. The price of a grilled lamprey in shops was about 3 Fmk (0.72 US $).

EFFECTS OF CHANGES OF ENVIRONMENT UPON RIVER LAMPREY STOCKS

Stocks of river lampreys are dependent on their spawning rivers. In Finland, most lamprey rivers have been affected by engineering works and so spawning migration has been prevented or spawning areas have been destroyed.

Construction of hydroelectric power stations has reduced the spawning areas of river lampreys in most rivers. The lowest power station is often near sea level so that there is no possibility of lampreys ascending the river to reproduce. In rivers where the lowest dam is higher in the river, the circadial or seasonal regulation of water levels by the power stations destroys lamprey larvae by drying or freezing. In rivers where there is only one power station or there are rapids between the two lowest power stations, it is possible to transport spawners over the lowest dam to increase the available spawning area. This has proved to be useful in the Kemijoki and Iijoki rivers where lamprey stocks have been maintained so that commercial fishing is still possible (Tuikkala 1974). In those rivers where there are no rapids left, transport upstream is only useful where it is possible for lampreys to migrate into tributaries. For instance, in the Oulujoki River, 7500 spawners were transported in 1975 to a small tributary situated about 30 km from the sea. Spawning was successful in this tributary and lamprey larvae were found in September 1976 near the areas of release (Salojärvi et al. 1978).

During the first half of this century most of the rapids in rivers flowing to the Baltic Sea were cleared for timber floating from inland forests to the coast. This greatly diminished the numbers of rapids and thus the spawning areas for river lampreys. Through some rapids a narrow channel was dug. The other rapids were left dry or the water velocities became so slow that lampreys do not spawn there.

The construction of artificial lakes and ponds in the upper parts of water courses for storing water for hydroelectric power stations has caused damage to lamprey stocks. These lakes and ponds have been built on marshy land and oxygen concentrations remain at a low level for many years because of the decomposition of organic material. In many of these reservoirs water is abstracted from the lower layers which are almost devoid of oxygen. This must increase the mortality of lamprey larvae and other organisms in rivers. Effluents from factories and communities cause similar harmful effects.

Other factors have also been assumed to affect lamprey stocks. In the Kymijoki River in the Gulf of Finland, fishermen have observed that the building of a new bridge with bright street lights has prevented lampreys migrating upstream of the bridge. The bright lights, which illuminate the whole bed of the river, are thought to be responsible. Illumination is thought to resemble moonlight, which also affects lamprey behavior. No research on this subject, however, has been carried out in Finland. Russian fishermen have used light to guide lampreys into the traps (Abakumov 1956).

Discussion

River lampreys have a great economic importance in Finland but man-made changes in rivers threaten the existence of lamprey stocks. River lamprey scars have been found on valuable fish species but no effects on fish stocks have been reported. For this reason, river lamprey stocks should be strengthened. There are many possible ways of doing this, for example, by transporting spawners over dams, by demanding better sewage treatment, by reducing water level regulation in spawning rivers, and by building lamprey-ways into power stations and dams. Artificial rearing of river lampreys should also be considered if other implementations are not sufficient.

Sea lamprey are rare in Finland. Most of the captures have been on the southern coast and only a few in rivers. In Finnish rivers there are no sea lamprey stocks, and no information about sea lamprey spawning populations in the Baltic has been published. The reason for this is not known and it would seem perfectly possible for sea lampreys to establish stocks in the Baltic Sea. Probably the number of sea lampreys migrating into the Baltic Sea is too small to start a viable population, and because of the small numbers no damage to stocks has been reported.

Brook lampreys have no parasitic phase, and are thus harmless to fish stocks in inland waters. Landlocked river lampreys do have a parasitic phase and scars have been found on valuable fish species, but effects on fish stocks have not been reported. Sea lampreys, landlocked river lampreys, and brook lampreys are of no interest to the fishing industry and of no economic significance.

Acknowledgments

The authors thank Dr Lauri Koli and Mr Alpo Tuikkala for materials and discussions, Miss Eija Nylander for drawing the figures, and Mr Leigh Pleaster for checking the English.

Abakumov, V. A. 1956. The mode of life of the Baltic river lamprey. Vopr. Ikhtiol. 16: 133–138.

1960. Reasons for the similarity in the ecology of the Petromyzonidae and Salmonidae. Nauchn. Dokl. Vyssh. Shk. Biol. Nauki 3: 25–28.

Andersson, E. 1980. Merilohen ravinnosta syyspyyntikauden aikana itäisellä Suomenlahdella. Riista- ja kalatalouden tutkimuslaitos. Tiedonantoja 15: 40–47.

Berg, L. S. 1948. Freshwater fishes of the USSR, and adjacent countries. Guide to the Fauna of the USSR, No. 27, Zoological institute. Acad. Sci. USSR. (Transl. from Russian by Israel Program for Sci. Transl., Jerusalem, 1961)

Hardisty, M. W., and I. C. Potter. 1971. The behaviour, ecology and growth of larval lampreys, p. 85–120. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Academic Press, London and New York.

Hurme, S. 1966. Nahkiaisjoet Suomen rannikolla. Suomen Kalastusl. 5: 135–139.

Ivanova-Berg, M. M. 1936. Spring migration and spawning of the river lamprey. Izv. Akad. Nauk SSSR 1936. 599–604. (In Russian: English summary)

Koli, L. 1963. Sisävesissämme mereen vaeltamaton nahkiaiskanta, *Lampetra fluviatilis*? Luonnon Tutkija 67: 20.

1969. Eräistä kalastomme taksonomisista kysymyksistä. Luonnon Tutkija 73: 93–105.

1975. Retkeilijän kalaopas. Otaua Keuruu. 127 p.

Salojärvi, K., H. Auvinen, and E. Ikonen. 1978. Oulujoen vesistön kalataloussuunnitelma. Duplicate, Finnish Game Fish. Res. Inst.

Sirelius, U. T. 1908. Suomalaisten kalastus III. Suomal Kirjall. Seur. toim 116: 259–459.

Storå, N. 1978. Lamprey fishing in the rivers of the Gulf of Bothnia. *In* N.-A. Bringius [ed.] Ethnologia Scandinavica. J. Nordic Ethnol. 1978: 67–98.

Tuikkala, A. 1971. Nahkiaisen elintavoista ja sen pyynnistä Pyhäjoella. Kalatalous-säät. Monist. Julk. 40: 1–59.

1974. Kemijoen nahkiaissaaliit ennen ja jälkeen Isohaaran padon rakentamisen. Suomen Kalastusl. 80: 50–55.

Valtonen, T., and M. Tossavainen. 1978. Nahkiaisen poikastuotantoalueet. *In* T. Valtonen and K. Kuusela [ed.] Lestijoen luonnontalouden elvyttämisen edellytykset. Duplicate, University of Oulu, Finland.

Wigren, B.-J. 1954. Dygnsrytmiken hos nejonögat (*Petromyzon fluviatilis* L.) Memo. Soc. Fauna Flora Fenn. 29: 24–27.

1964. Om nejonögonen i Kumo älv. Fiskeritidskr. Finland 2: 1–3.

Distribution and Abundance of European River Lamprey (*Lampetra fluviatilis*) Larvae in Three Rivers Running into Bothnian Bay, Finland[1]

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KAINUA K., AND T. VALTONEN. 1980. Distribution and abundance of European river lamprey (*Lampetra fluviatilis*) larvae in three rivers running into Bothnian Bay, Finland. Can. J. Fish Aquat. Sci. 37: 1960–1966.

Larvae of parasitic European river lamprey (*Lampetra fluviatilis*) were studied in the Kalajoki, Pyhäjoki, and Siikajoki rivers which flow into Bothnian Bay in Finland. In the Kalajoki river, ammocoetes occur up to 40 km upstream from the mouth, but in the Pyhäjoki rapids block most of the adult migration about 20 km from the river mouth. The Siikajoki river is blocked by a hydroelectric dam 16 km from the estuary. The mean abundance of larvae in 1977 was 12/m² in the Pyhäjoki and 21/m² in the Siikajoki river. In 1978 the mean abundance was 6/m² in the best area (an 8-km stretch) of the Kalajoki, 15/m² in the Pyhäjoki, and 21/m² in the lower 7 km of the Siikajoki river. The mean length of larvae was smallest in the Siikajoki (45 mm in 1977 and 55 mm in 1978) and largest in the Kalajoki river (77 mm in 1978). Reasons for such size differences and the variation in year-class strengths may be attributable to oxygen deficiencies and other problems caused by dams and other construction work on the rivers. Both the Siikajoki and Kalajoki rivers appear to be affected in this way. The Pyhäjoki appears to be the least disturbed of the three rivers. Ammocoetes favor mean grain sizes from 0.05 to 0.10 mm. Myomere studies on larvae from the Siikajoki river gave a mean count of 62.3 (range, 60–64) and verified that the larvae involved were those of the river lamprey.

Key words: lamprey, Finland, larvae, ammocoete, *Lampetra fluviatilis*, European river lamprey

KAINUA K., AND T. VALTONEN. 1980. Distribution and abundance of European river lamprey (*Lampetra fluviatilis*) larvae in three rivers running into Bothnian Bay, Finland. Can. J. Fish Aquat. Sci. 37: 1960–1966.

Les larves de la lamproie fluviatile européenne (*Lampetra fluviatilis*) parasite ont été étudiées dans les fleuves Kalajoki, Pyhäjoki et Siikajoki qui se déversent dans le golfe de Botnie, en Finlande. Dans le Kalajoki, il y a des ammocètes jusqu'à 40 km de l'embouchure, mais dans le Pyhäjoki, les rapides bloquent le gros de la migration des adultes à environ 20 km de l'embouchure du fleuve. Un barrage hydroélectrique à 16 km de l'estuaire bloque le Siikajoki. L'abondance moyenne des larves en 1977 était de 12/m² dans le Pyhäjoki et de 21/m² dans le Siikajoki. En 1978, l'abondance moyenne était de 6/m² dans le meilleur secteur (de 8 km de long) du Kalajoki, 15/m² dans le Pyhäjoki et 21/m² dans les 7 km inférieurs du Siikajoki. La plus petite longueur moyenne des larves se trouve dans le Siikajoki (45 mm en 1977 et 55 mm en 1978), et la plus grande se trouve dans le Kalajoki (77 mm en 1978). De telles différences de taille et les fluctuations d'abondance des classes d'âge peuvent être attribuables à des déficiences d'oxygène et autres problèmes causés par les barrages et autres constructions dans ces fleuves. Le Siikajoki et le Kalajoki semblent tous deux affectés de cette manière. Des trois fleuves, le Pyhäjoki est celui qui semble le moins dérangé. Les ammocètes préfèrent un substrat dont les grains ont des tailles de 0,05 à 0,10 mm. Les larves du Siikajoki ont un nombre moyen de myomères de 62,3 (extrêmes, 60–64), ce qui confirme que ces larves sont bien celles de la lamproie fluviatile européenne.

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IN their review of lamprey ecology and fishing in Finland, Tuunainen et al. (1980) gave cogent reasons why an intensive study of the European river lamprey (*Lampetra fluviatilis*) is necessary. Lamprey stocks have been reduced to very low numbers in southern Finland, and in those rivers running into Bothnian Bay they have also declined greatly as a result of extensive construction work within the rivers. In central Ostrobothnia, that is the middle part of the Bothnian Bay coast, lamprey fishing is the last effective traditional way of river fishing being carried out in all the

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TABLE 1. Main hydrological features of the study rivers.

River	From source lake, length (km)	Annual discharge, $m^3 \cdot s^{-1}$			Drainage area (km^2)	Height of source lake (m)
		Mean	Max.	Min.		
Siikajoki	152	34	400	2.2	4259	95
Pyhäjoki	162	30.8	145	3.9	3733	140
Kalajoki	130	35.6	236	3.0	4200	81

rivers of the area, from the Lestijoki to the Siikajoki (Hurme 1966; Tuikkala 1971; Klapuri 1972; Tuunainen et al. 1980). Extensive water regulation works already carried out or planned, for the Kalajoki, Pyhäjoki, and Siikajoki have led to a study of lamprey ecology and the importance of fishing in these rivers, and also in Lestijoki where the resuscitation of all kinds of fisheries is being attempted (Valtonen and Niemi 1979). The present paper deals with the distribution and ecology of river lamprey ammocoetes in the Kalajoki, Pyhäjoki, and Siikajoki rivers. With any work on river lamprey larvae, one must also consider the brook lamprey because of their possible occurrence in the same sections of rivers (Tuunainen et al. 1980).

Study Area

The study rivers are situated in the central part of western Finland (Valtonen 1980) and they all run into the middle part of Bothnian Bay. They lie between 64 and 65°N and are ice-covered from November until the beginning of May. All the rivers are comparatively small; their mean discharge varies from 31 to 36 $m^3 \cdot s^{-1}$, but the annual minima and maxima are very different (Table 1). One reason for the latter phenomenon is the small number of lakes in the watersheds.

In all these rivers, which drain peatland, the water is rich in humus, especially during the spring, and in recent years construction works have seriously affected water quality. Dams for flood protection and hydroelectric power have been constructed on the Kalajoki and Siikajoki rivers. On the Kalajoki, the Hautaperä dam was completed in 1975 and first used during the winter of 1975/1976; on the Siikajoki, the Uljua dam was finished in 1969 and used the next winter. As a result, humic materials have been washed into many parts of both rivers and serious oxygen deficiencies have been recorded (Table 2). Very high iron concentrations have also been found, especially in the Siikajoki River (Table 2).

Methods

Field work on ammocoetes was carried out during the summers of 1977 and 1978. Samples were taken at intervals of 0.5 km (±25 m) and from both sides of the river, the distances being measured from the map and modified slightly according to access to the river bank. Samples were taken from the rivers edge down to a depth of 80 cm. Fairly normal summer water levels occurred during the study period, except when the Kalajoki river flooded in 1977.

In the Kalajoki river samples were taken along about 55 km of the river as far as Raudaskylä in the parish of Nivala, with some pilot samples from the upper river. The Pyhäjoki river was sampled as far as the city of Oulainen, about 50 km from the sea. However, in these rivers the upper reaches were sampled less intensively than the lower

TABLE 2. Specifications of some river water parameters at critical times in the study rivers.

Place	O_2%, saturation minimum	Fe, mg/L maximum	Time	Main reason	Reference
Kalajoki river (40 km upstream from the estuary)	10	7	Winter 1977	Two emptyings of the Hautaperä basin	Jokinen 1977 Kilpinen 1979
Pyhäjoki river					
Middle part	68	4.9	Winter and summer for O_2, spring for Fe, during the years 1962–77 recorded seasonally		National Water board, Oulu District, listed tables
Lowest rapid	70	3.9			
Siikajoki whole river		97.2	Summer 1969	Construction of Uljua basin	"
	0–10		Winter 1970	First emptying of Uljua basin	Myllymaa 1978
Ruukki ~25 km from the river mouth	21	8	Winter 1977	First emptying of Uljua basin	Myllymaa 1978

(see Fig. 1 and 2). The Siikajoki river was sampled only as far as the Pöyry hydroelectric station which blocks the river 16 km from its mouth.

A shovel, with a collecting area of about 200 cm², was used to search for larvae. If they were found, an Ekman–Birge grab (area of 273 cm²) was used from 5 to 10 times for a quantitative sample. The sampler was pushed down into the mud or silt for at least 10 cm and then closed. Electric-shocking equipment proved to be impractical for quantitative work, because of the escape of larvae and the fact that younger ones possibly did not leave the mud. Sieving was carried out immediately with a 1.5-mm mesh sieve. No special attempt was made to catch larvae that hatched during the study year because these larvae were only about 1 cm in length (Tuikkala 1971; Tuunainen et al. 1980) and would have escaped through the sieve.

The larvae were anesthetized in MS 222, measured to the nearest millimetre, and preserved in 5% formalin. Weight measurements were made from preserved specimens after about 2 w, the larvae being dried for about 30 s on absorbent paper before weighing.

A small propeller device was used for measuring current speeds at some of the sampling sites. Measurements were made 10 cm above the river bottom where there was an appreciable current. Near the bank, current velocities were often too low to be detected by the meter, and measurements were made with a float just below the water surface. In the summer of 1977 substrate samples were also taken for particle size determination. Samples were taken with an iron tube (about 3 cm) to a depth of 5 cm thus avoiding any deeper hard material. Standard laboratory sieves with meshes decreasing (always by half) from 8 to 0.125 mm plus a bottom sieve of 0.074-mm mesh were used. Before this dry sieving, however, wet sieving with a 0.053-mm sieve was carried out. The results are expressed as median particle sizes (D_{50}).

Distribution and Density of the Larvae

KALAJOKI RIVER

Inventory of the Kalajoki river larval population during the summer of 1977 was considered unsuccessful (Fig. 1) because of a summer flood during the sampling period. This meant that the necessary accuracy in finding the right sites could not be achieved. In 1978 the main area occupied by larvae was from Pitkäisenkylä to Tilvisperä, 6–14 km from the river mouth. In this area the mean density was 5.7 larvae/m². A small but denser occurrence was found 40 km from the river mouth, at four sampling sites below the town of Ylivieska (Fig. 1) where 15 larvae/m² were found. Just upstream from this town considerable dredging had been carried out in previous years. In the estuary, which has a length of about 5 km, the river has no suitable substrate for lamprey larvae, being mainly stony. This area of the river contained a mean of only 0.7 larvae/m².

PYHÄJOKI RIVER

The number of ammocoetes in the Pyhäjoki river was rather similar in both 1977 and 1978 (Fig. 2). All habitable parts of the river, as far upstream as the

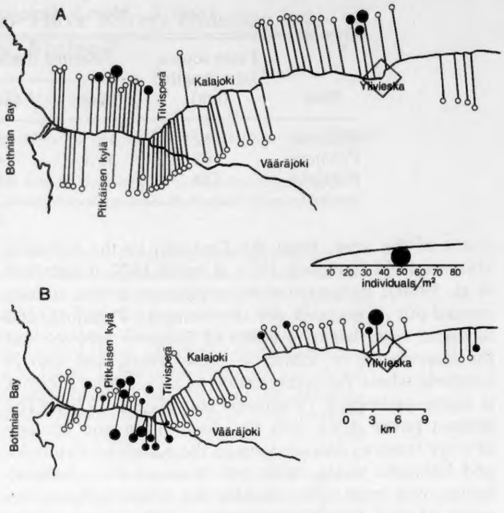

FIG. 1. Abundance of ammocoete larvae/m² in sampling sites at Kalajoki in 1977 and 1978. Open circles: no larvae were found. A = 1977, B = 1978. X = no sampling because of unsuitable substrate.

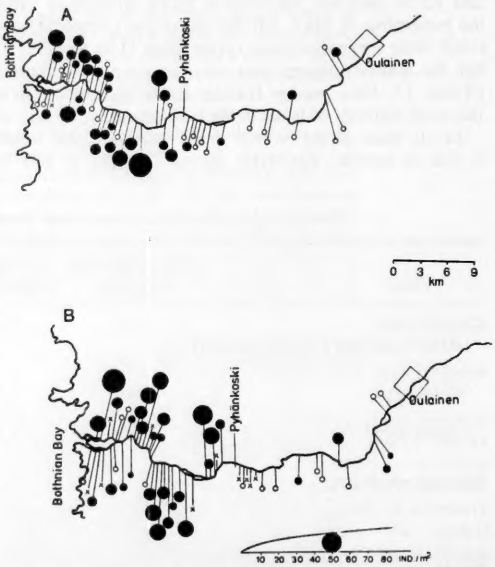

FIG. 2. Density of ammocoete larvae in sampling sites in Pyhäjoki in 1977 and 1978. For other explanations see Fig. 1.

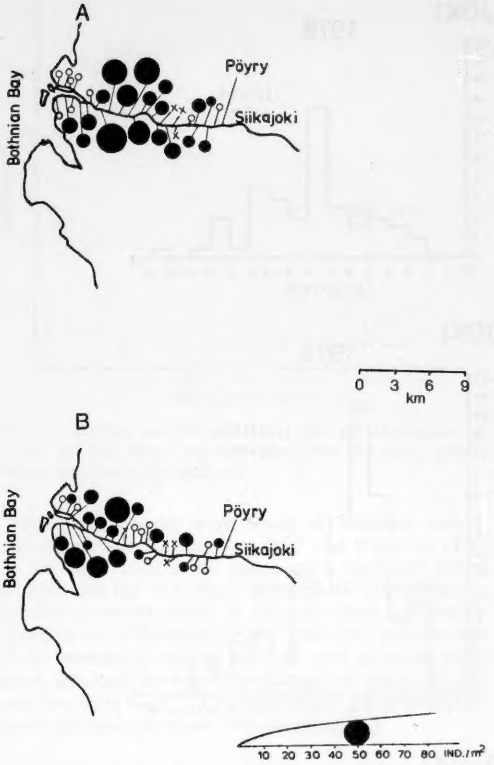

FIG. 3. Density of ammocoete larvae in sampling sites in Siikajoki in 1977 and 1978. For other explanations see Fig. 1.

Pyhänkoski rapids, had similar densities of larvae. At the river mouth the water is brackish and no larvae occur. A density of 11.8 larvae/m^2 in 1977 and 15.3 larvae/m^2 in 1978 was observed between the river mouth and the Pyhänkoski rapids. Above the rapids the density of larvae was much less: 3.2/m^2 according to the work carried out in 1977, and 1.7/m^2 in 1978.

SIIKAJOKI RIVER

In this river the ammocoetes were found as far upstream as the Pöyry dam (Fig. 3), beyond which adults cannot migrate upstream. Ammocoetes were found in high densities from the dam to the river mouth, a distance of about 16 km, in all those places favorable for larvae. The highest densities were found in a stretch 4–8 km upstream from the river mouth. In 1977, 21.3 larvae/m^2 were found throughout the area downstream of the Pöyry dam, but in 1978 this density occurred only in the lower half of the river (7 km). In the upper half, as far as the dam, the density was only four larvae/m^2. The water level was very low in 1978, and as a result the area suitable for burrowing ammocoetes was greatly restricted.

Frequency of Length-Classes

Length frequency distributions (Fig. 4) show clear peaks for two or three age-groups. Larvae in the youngest age-group will mostly have slipped through the sieve (1.5-mm mesh). Therefore, the minimum age necessary for transformation in the river phase is thought to be 4 yr. Ammocoetes exceeding 120 mm in length may well have reached 6–7 yr in the larval phase and are possibly *L. planeri*.

There is a significant difference in the size of some year-classes, especially the 1976 year-class in the Kalajoki compared with those in the Pyhäjoki and Siikajoki rivers (Fig. 4). In the Kalajoki the numbers in this year-class (and young larvae in general) are very low. The 1976 year-class was very numerous in Pyhäjoki and Siikajoki. In 1977, when only a few were caught from the Kalajoki river (because of floods), their mean length was 95 mm ($n = 8$) and in 1978, 77 mm ($n = 55$). In Pyhäjoki the comparable values were 58 mm ($n = 108$) and 65 mm ($n = 122$) and in Siikajoki 45 mm ($n = 128$) and 55 mm ($n = 78$), respectively.

Water Velocity

Rivers running into Bothnian Bay generally have a low gradient, with a mean of less than 1 in 100. The middle section usually runs through a floodplain, while the water that enters the sea in the estuary flows through newly deposited sediment, for the land in this area is rising at a constant rapid rate of about 9 mm per year. However, the current speed does not increase in proportion to the rate of land upheaval because this phenomenon is greatest in the coastal areas.

According to map studies, the gradient in those areas mainly occupied by lamprey larvae was 1–2 in 100. Water velocities, measured in midstream in the areas occupied by larvae, ranged from 1–5 cm/s to about 50 cm/s, with small larvae being proportionally more numerous in habitats where the flow was rapid. Where larvae were found in shallow water the rate of flow was almost constantly below 10 cm/s. These speeds were all measured under summer conditions, however. In winter, with low or very low water levels, the current speed may be less, and during the spring flood it is much higher.

Particle Size in the Ammocoete Habitat

Ammocoetes were usually found, in fine sand or silt banks, most frequently in places where there was an accumulation of organic material. Places where floodwaters back up were especially favored.

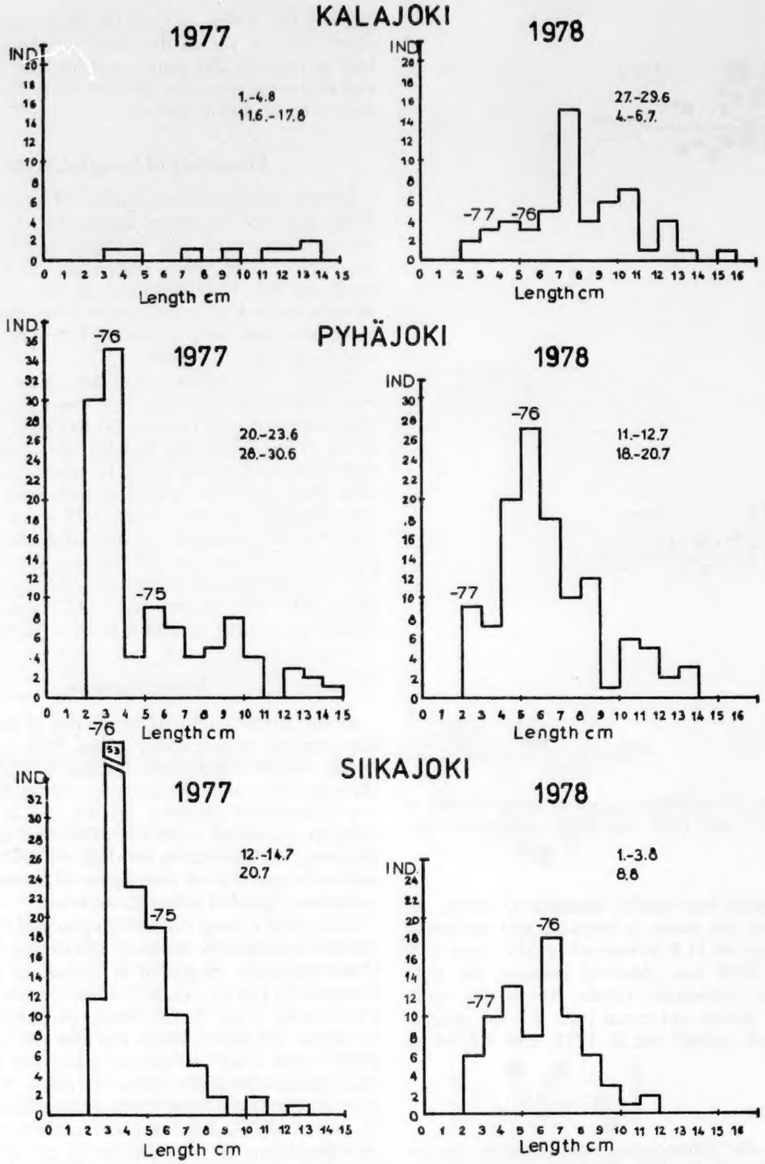

FIG. 4. Distribution of different-sized larvae in the study rivers in 1977 and 1978. One-centimetre size-classes are given. Sampling time is shown for every river and year separately. In most figures the peaks of the two youngest year-classes are indicated by the birth year of the year-class.

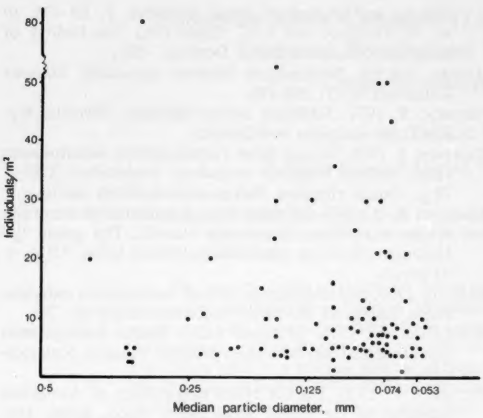

FIG. 5. Median particle size (D_{50}) and the abundance of larvae. In this figure only samples from the areas where larvae were found are included.

Most ammocoetes were found in substrate with a median particle size between 0.05 and 0.20 mm (Fig. 5). In the present study ammocoetes were not found in finer material (i.e. clay) although an occasional individual occurred earlier in one clay bank in a neighboring river. Differences in the preferred particle size of the burrowing areas of different sizes of larvae were small, although the largest larvae seem to prefer smaller particles (soft banks). The age-group 0, known to occur mainly in sandy biotopes, was not sampled.

Myomere Studies

Myomeres were counted in all larvae longer than 50 mm taken from the Siikajoki river. The mean number was 62.3 (range 60–64), which corresponds to known values for the river lamprey (Potter and Osborne 1975). Metamorphosis occurred in three larvae of 101, 106, and 124 mm (July 26, 1978).

Discussion

RIVER WATER AND AMMOCOETE PRODUCTION

Although the rivers studied have a low gradient and a small mean discharge, they have been involved in very extensive water regulation schemes for flood protection and hydroelectric power production. In both the Siikajoki and Kalajoki rivers small reservoirs (the Uljua and Hautaperä basins) have been built. In Siikajoki during construction, high iron concentrations were found in the river and, later, during winter, when the basin was allowed to empty completely, a severe lack of oxygen was recorded. This is considered to have spread through the whole river by 1970. Even during the winter of 1977 a low oxygen concentration minimum of 21% was measured (Table 2, Myllymaa 1978). Downstream of the automatic measuring equipment there is, however, a hydroelectric dam which may aerate the water to some extent. In the 1970s in this river, good year-classes of lamprey did not occur until 1975 or 1976. This can be seen in the low mean size of the Siikajoki sample (45 mm) compared with that of the Pyhäjoki larvae (58 mm).

In the Pyhäjoki river effective water regulation devices have also been constructed, but they involve only the building of two hydroelectric dams which were completed in the autumn of 1978. Following this, long stretches of the river bed in the upper sections were removed. In the 1950s and 1960s there was considerable construction for flood protection, leading to lethal pH conditions by the beginning of the 1960s. However, during the study period conditions probably represented the "normal" or natural (population) levels fairly accurately.

In the Kalajoki river, both the long-term minimum oxygen and the maximum iron concentration values were reached in the winters of 1976 and 1977 when the Hautaperä basin was impounded. In addition, large-scale dredging work began at the same time, which, especially in the winter of 1977, was carried out just upstream of the highest and most densely populated lamprey beds (Jokinen 1977; Kilpinen 1979). Thus, the area dredged in 1977 could no longer be studied in the summer of 1978. As a consequence, very few young ammocoetes were found in the studies in 1977 and 1978.

The number of lampreys captured in the autumn spawning migrations diminished during 1976–78 to less than half of former levels. However, this is not considered to be a very important factor when the virtual absence of the 1976 year-class is considered.

In addition to the difficulties of the over-wintering adults and the threat to larvae from low oxygen and high iron concentrations, larvae may also be destroyed by drifting downstream into the sea. The period of transformation and seaward migration is also a dangerous one, for there are a number of major physiological changes at this critical time (Damas 1935; Gritsenko 1968; Hardisty and Potter 1971). A decrease in the number of larvae in Kalajoki may be expected from 1982 onwards if breeding continues to be unsuccessful, as demonstrated in present study for 1976–77. Some adults may spawn in different rivers from the one in which they were born as a result of the deteriorating quality of the water.

DISTRIBUTION OF LARVAE IN RIVERS

In Finnish rivers the most densely populated nursery for larvae areas may be as far upstream as 30 km (as in Lestijoki) or even 40 km from the sea (as in part of Kalajoki). The longer the distance, however, the greater are the hazards in both upstream and downstream migration. The headwaters of the great rivers of northern Finland are well populated by brook lampreys, and lampreys also occur in the headwaters behind hydroelectric power dams which block some rivers (Valtonen and Niemi 1979). Studies to determine whether or not there are now landlocked populations (Koli 1963) have not yet been carried out. There is now some evidence that the number of lampreys over 150 mm long is greater in the upper parts of the river, which indicates the existence of a population of brook lampreys. In the present study the relative number of larger lampreys (90–120 mm) did not increase downstream (Baxter 1954; Thomas 1962; Potter 1970) as is known to occur in some rivers with a steep gradient (Baxter 1954).

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Many of the staff of the National Water Board, Oulu District, helped us with the work; Mr Mikko Kerãnen has been especially involved. Mr Asko Niemi from the National Water Board, Kokkola District, has given advice, and Mr Lauri Alatalo (from the same office) has participated in most of the field work. In addition to them we are grateful to Dr Sheila Hicks for translation of the text. Professor Ian C. Potter kindly considered and discussed with us the age-group distribution of our ammocoete material.

BAXTER, G. W. 1954. Studies on the biology of lampreys. Ph.D. thesis, London University, England.

DAMAS, H. 1935. Contribution a l'étude de la tete de la lamproie. Arch. Biol. Paris 46: 171–227. (cited in Hardisty and Potter 1971)

GRITSENKO, O. F. 1968. [On the question of an ecological parallelism between lampreys and salmon.] Izv. Tikhookean. nauchno-issled. Inst. Ryb. Okeanogr. 65: 157–169. (In Russian) (cited in Hardisty and Potter 1971)

HARDISTY, M. W., AND I. C. POTTER. 1971. The behavior, ecology and growth of larval lampreys, p. 85–125. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Academic Press, Dorking. 423 p.

HURME, S. 1966. Nahkiaisjoet Suomen rannikolla. Suomen Kalastuslehti 73: 135–139.

JOKINEN, S. 1977. Kalajoen veden laadusta. Moniste, 6 p. Kokkolan vesipiirin vesitoimisto.

KILPINEN, I. 1979. Vesistötöiden työnaikaisesta vaikutuksesta veden laatuun Kalajoen vesistössä. Diplomityö. XIII + 79 p., Oulun yliopisto, Rakentamistekniikan osasto.

KLAPURI, K. J. 1972. Kalastuksesta ja kalanmarkkinoinnista erityisesti eteläisen Perämeren alueella. Pro gradu työ Helsingin yliopiston maatalouspolitiikan laitos, 321 p. + 72 liitettä.

KOLI, L. 1963. Sisävesissämme mereen vaeltamaton nahkiaiskanta, Lampetra fluviatilis? Luonnon tutkija 67: 20.

MYLLYMAA, U. 1978. Siikajoen veden laadun kehittyminen Uljuan altaan käyttöönoton jälkeen. Suomen Kalastuslehti 5: 122–124.

POTTER, I. C. 1970. The life cycles and ecology of Australian lampreys of the genus *Mordacia* J. Zool., Lond. 161: 487–511.

POTTER, I. C., AND T. S. OSBORNE. 1975. The systematics of British larval lampreys. J. Zool., Lond. 176: 311–329.

THOMAS, M. L. H. 1962. Observations on ecology of ammocoetes *Petromyzon marinus* L. and *Enthosphenas Lamottei* (Le Sueur). M.Sc. thesis, University of Toronto, Canada. (Cited in Hardisty and Potter 1971)

TUIKKALA, A. 1971. Nahkiaisen elintavoista ja sen pyynnistä Pyhäjoella. Kalastussäätiön monistettuja julkaisuja 40: 1–59.

TUUNAINEN, P., E. IKONEN, AND H. AUVINEN. 1980. Lampreys and lamprey fisheries in Finland. Can. J. Fish. Aquat. Sci. 37: 1953–1959.

VALTONEN, T. 1980. European river lamprey (*Lampetra fluviatilis*) fishing and lamprey populations in some rivers running into Bothnian Bay, Finland. Can. J. Fish. Aquat. Sci. 37: 1967–1973.

VALTONEN, T., AND A. NIEMI. 1979. The present state of fishing in Lestijoki, a small river in Finland. Verh. Int. Verein. Limnol. 20: 285–2091.

European River Lamprey (*Lampetra fluviatilis*) Fishing and Lamprey Populations in some Rivers Running into Bothnian Bay, Finland[1]

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VALTONEN, T. 1980. European river lamprey (*Lampetra fluviatilis*) fishing and lamprey populations in some rivers running into Bothnian Bay, Finland. Can. J. Fish. Aquat. Sci. 37: 1967–1973.

The coastal region of Bothnian Bay is now the center of fisheries for European river lamprey *Lampetra fluviatilis* in Finland. This species has been studied in the Kalajoki and Pyhäjoki rivers and data are also available from the Lestijoki River. In the Kalajoki River in 1977, 30 fishermen operating 70 trap nets and 900 basket traps caught about 134 000 lampreys. Fewer traps were used by a smaller number of fishermen in 1978, but the catch remained the same. In the Pyhäjoki River in 1977, 50 fishermen operating 50 trap nets and 330 basket traps caught 184 000 lampreys. In 1978 fewer traps were used by a smaller number of fishermen and the catch was 93 000 lampreys. Tagging indicated that about 80% of the upstream migrants (estimated at 200 000 in 1977) were being captured in the Kalajoki River, but only about 65% in the Pyhäjoki River (estimated at 400 000 - 500 000 in 1977). Reasons for the differences between rivers and years are discussed.

Key words: Lampetra fluviatilis, Finland, fishery, rivers

VALTONEN, T. 1980. European river lamprey (*Lampetra fluviatilis*) fishing and lamprey populations in some rivers running into Bothnian Bay, Finland. Can. J. Fish. Aquat. Sci. 37: 1967–1973.

La région côtière du golfe de Botnie est maintenant le centre de la pèche de la lamproie fluviatile européene *Lampetra fluviatilis* en Finlande. Cette espèce a été étudiée dans les fleuves Kalajoki et Pyhäjoki, et l'on possède égelement des données pour le Lestijoki. Dans le Kalajoki en 1977, 30 pêcheurs exploitant 70 filets-trappes et 900 paniers capturèrent environ 134 000 lamproies. En 1978, un nombre moindre de pêcheurs utilisèrent moins d'engins, mais les prises demeurèrent les mêmes. Dans le Pyhäjoki en 1977, 50 pêcheurs exploitant 50 filets-trappes et 330 paniers capturèrent 184 000 lamproies. En 1978, un nombre moindre de pêcheurs utilisèrent moins d'engins, et les prises furent de 93 000 lamproies. L'étiquetage indique qu'environ 80% des sujets émigrant vers l'amont (estimés à 200 000 en 1977) ont été capturés dans le Kalajoki, mais seulement environ 65% dans le Pyhäjoki (estimés à 400 000–500 000 en 1977). On examine les raisons de ces différences entre fleuves et années.

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THE study of diadromous fish populations, following comparatively rapid changes in the quality of river waters due to the influx of wastes and humic-rich water from peat lands and to regulatory constructions closing off migration routes, is of continuous scientific importance and economic value. In Finland, the European river lamprey, *Lampetra fluviatilis*, is the last remaining anadromous species that is possible to catch in large numbers in most of the rivers running into Bothnian Bay. The continued building of reservoirs and hydroelectric plants along these rivers has made it essential to assess lamprey populations there, and the fisheries dependent on them.

Study Area

The present work concentrates on the Kalajoki and Pyhäjoki rivers (Fig. 1) which run into the central part of Bothnian Bay, the northern part of the Gulf of Bothnia in the Baltic Sea. Information about lamprey fisheries on a neighboring river to the south, the Lestijoki, is also presented. During the study years the Kalajoki and Pyhäjoki rivers were open for the lamprey migration but the Kalajoki River already had a reservoir as its headwaters. Both rivers have some hydroelectric plants in connection with or near their source lakes (Fig. 1). The Pyhänkoski rapids (Fig. 1) on the Pyhäjoki is steep and seems to prevent lampreys going further upstream. In the Lestijoki River,

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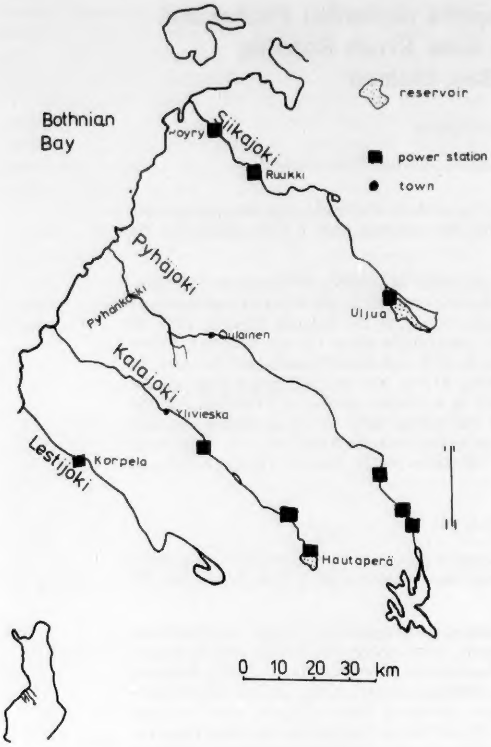

FIG. 1. The study rivers and main municipal centers along them, with the neighboring northern river, Siikajoki. Hydroelectric power stations and man-made lakes are also shown.

Korpela's dam has stopped lampreys going beyond 30 km from the estuary since 1921. Some characteristics of the rivers are as follows:

	Length, km	Height of source lake, m	Mean discharge, $m^3 \cdot s^{-1}$
Lestijoki	72	140	11.5
Kalajoki	130	81	35.6
Pyhäjoki	162	140	30.8

Additional details are presented by Kainua and Valtonen (1980). When the water is humic it may have a high iron concentration, especially in connection with dam construction. If there is a reservoir upstream that empties during the winter, low oxygen concentrations will be experienced at that time (for details see Kainua and Valtonen 1980).

Methods

Statistics for lamprey fishing were gathered by distributing catch diary forms which were later collected back from the fishermen. In addition to the daily fishing tackle used and the daily catch, the number of tagged lampreys was also entered on these forms.

TABLE 1. Numbers of lampreys handled by stock dealers from the Kalajoki and Pyhäjoki rivers in the 1970s.

	Kalajoki		Pyhäjoki	
Year	Stock dealers	Present study	Stock dealers	Present study
1971	229 000		144 000	
1972	~160 000		~150 000	
1973	121 000		94 000	
1974	124 000		158 000	
1975	195 000		196 000	
1976	139 000		136 000	
1977	108 000	134 000	156 000	185 000
1978	109 000	134 000	80 000	93 000

Tagging was done either by finclipping, or by a modification of a wire and plate tag, where comparatively strong (1 mm) wire was used and the plate was replaced by a small colored plastic bead whose number and color were changed for different experiments. The tag was applied by A. Tuikkala in the Finnish Game and Fisheries Research Institute.

Lamprey baskets used in the Pyhäjoki area are of willow (*Salix* sp.), which disintegrates in a relatively short time (3–5 yr) for which reason they are generally not kept in water during the day. At Kalajoki, in contrast, the age of the baskets was usually more than 30 yr, these being made of juniper (*Juniperus communis*). Usually they were kept in the water continuously, which makes it possible for one man to handle many more baskets. Several of them were also tied together for ease of handling.

Results

CATCHES IN THE 1970s

Some information about catches before the 1970s is available but the data does not give any good indication of population numbers. Trap net fishing began in the 1960s.

The catches bought by stock dealers after 1970 are known (Table 1), and the catches in 1971 have been studied in detail (Klapuri 1972). The proportion of catch handled by stock dealers has, at least to some extent, increased during 1977 and 1978 when it was 75% and 74% at Kalajoki and 80% and 82% at Pyhäjoki, respectively. When the price paid for lampreys prepared at home did not rise as much as that paid for fresh lampreys to fishermen, obviously more lamprey were purchased through the dealers.

In good lamprey years in the first half of the 1970s, a part of the catch was taken to mink farms, at least in the Pyhäjoki area, because stocks dealers did not have enough facilities for processing the whole catch. Thus 30% should be added to the catch purchased through dealers (this is their own estimate) to give

TABLE 2. The number of fishermen and the yearly catch in the Kalajoki and Pyhäjoki rivers in 1977 and 1978 with reference to the gear used.

Year	All lamprey fishermen	Number of Units		Individual catches		Total
		Trap nets	Lamprey basket	Trap net fisheries	Basket fisheries	
			A. Kalajoki			
1977	30	71	903	68 000	66 000	134 000
1978	26	59	728	84 500	49 500	134 000
			B. Pyhäjoki			
1977	50	57	327	~115 500	~70 000	184 500
1978	45	50	254	66 500	26 500	93 000

an idea of the total catches in the 1970s. The estimate is in rather good agreement with the total catch reported by Klapuri (1972) for the year 1971 at Kalajoki: 308 000 individuals. However, in Pyhäjoki 100% must be added into the dealers' catch to give Klapuri's prediction of 290 000 individuals. Thus the total catch numbers estimated from Table 1 must be regarded as minimum rather than mean values for the catches.

The available data show a clear decrease in the total catch in both rivers up until 1978. In Kalajoki the catch was already small in 1976, and low in both 1977 and 1978. In Pyhäjoki the catch was abruptly reduced in 1978. In 1978 the catch was 44% of the maximum known at Kalajoki and 32% at Pyhäjoki (Klapuri 1972, Table 1), but when compared to the earlier calculated minimum catches, the catch in 1978 was apparently not so much smaller, 85% at Kalajoki and 76% at Pyhäjoki.

FISHING INTENSITY AND CATCH PER EFFORT

The number of fishing gear used was higher in Kalajoki than in Pyhäjoki, although the number of fishermen was greater at Pyhäjoki (Table 2). In 1978, a few more trap nets were used at Kalajoki, but the number of lamprey baskets used was three times greater at Kalajoki.

Exact comparison between the gear has not yet been made. Differences in the equipment used in the rivers are partly necessary because of the fishing sites. Trap nets have to be shallow in the Pyhäjoki where the mouth of the river is wide and so shallow that much of it is overgrown by high *Scirpus* vegetation. A narrow open flow in the middle is bordered with trap nets. In the Kalajoki River the mouth is rather deep (2–4 m), but not very wide. Trap nets span the greater part of this river.

When the size or the catch per effort and the fishing intensity is considered it is clear that in the Kalajoki River the number of fishing gear used is based on a previously larger population of lamprey (Table 1). In both 1977 and 1978 the catch was small, with the result that there was a reduction in fishing effort or even the cessation of fishing altogether by some fishermen. In the Pyhäjoki River a similar decrease in the catch occurred in 1978. The catch per effort was, in both 1977 and 1978 (Table 3), lower in the Kalajoki than in the Pyhäjoki rivers. The trap net catch per effort in the Kalajoki River was 40% of that in the Pyhäjoki River in 1977 but 78% in 1978 when the Pyhäjoki catch was reduced abruptly. The catch per trap net per day increased also from 16 to 23 lampreys between 1977 and 1978 in the Kalajoki River (Table 3).

In catches from lamprey baskets the difference between the catch per effort was high in both study years although the catch from the Pyhäjoki River decreased from four to nearly three lampreys per basket per day from 1977 to 1978. In the Kalajoki River only one lamprey was caught per basket per day in both years. In 1978 many of the fishermen whose baskets were situated highest in the river did not fish at all in the Pyhäjoki River in 1978, when the catch was small.

RESULTS FROM TAGGING EXPERIMENTS

The finclipping method shows a high rate of exploitation (u) for the Kalajoki population (Table 4). The percentage of recapture was 64–89 in September, the lower number at the beginning and the higher one at the end of the month.

The bead mark method gave an estimated fishing mortality of above 80% for the end of September. In the middle of October the rate of exploitation was still about 80% using both methods, but then decreased rapidly. This was because ice on the river prevented most of the trap net fishing at that time and some fishing with baskets. It should be noticed that neither of the methods used showed any clear difference in the rate of exploitation between the years 1977 and 1978 though there was a decrease in the fishing effort.

In September the fishing intensity remained almost constant and this allowed a comparison of the investigated catch with that of the whole month. In October the situation was reversed, when fishing intensity was greatly reduced towards the end of the month. A

TABLE 3. Catch per effort with trap nets and lamprey baskets in Pyhäjoki and Kalajoki in 1977 and 1978. Adequately detailed knowledge from efforts (catch per day from one trap net and basket) are included.

Month	Units of effort	Catch	Catch per effort	Units of effort	Catch	Catch per effort	Units of effort	Catch	Catch per effort	Units of effort	Catch	Catch per effort
	Trap net, Kalajoki 1977			*1978*			*Trap net Pyhäjoki 1977*			*1978*		
Aug.	755	2 375	3.1	474	1 539	3.2	203	3 096	15.3	326	2 209	6.8
Sept.	1 929	29 353	15.2	1 641	36 739	22.4	501	22 018	44.0	718	22 330	31.1
Oct.	1 307	32 935	25.2	1 464	43 444	29.7	320	17 386	54.3	463	19 353	41.8
Nov.	117	2 101	18.0				85	2 649	31.2			
Total	4 108	66 764	16.3	3 579	81 722	22.8	1109	45 149	40.7	1507	43 892	29.1
	Lamprey basket, Kalajoki 1977			*1978*			*Lamprey basket, Pyhäjoki 1977*			*1978*		
Aug.	10 046	1 091	0.1	5 863	685	0.1	1153	1 866	1.6	287	232	0.8
Sept.	21 830	11 509	0.5	15 351	13 110	0.9	3194	11 722	3.7	2005	6 306	3.1
Oct.	20 297	30 024	1.5	16 492	26 520	1.6	2843	12 441	4.4	1128	4 036	3.6
Nov.	6 100	12 048	2.0	1 085	1 177	1.1	455	4 953	10.9	180	808	4.5
Dec.	190	299	1.6									
Total	58 463	54 971	0.9	38 791	41 492	1.1	7645	30 982	4.1	3600	11 382	3.2

TABLE 4. Results from tagging experiments at the Kalajoki River in 1977 and 1978. The estimate of a part of population (N') counted according to the formula $(M + 1)(C + 1)/(R + 1)$ (Ricker 1975). R = the number of recaptured lampreys, u = rate of exploitation.

Date	Number marked M	Recapture %	Monthly catch		N'	u (%)
			Investigated C	Total		
Finclipping						
1977						
Sept. 8–9	817	53.4	36 084	44 538	67 545	65.9
Sept. 21	571	54.3	29 774	44 538	54 763	81.4
			Catch within 1–4 (5) d from tagging			
			Investigated C	Total		
Oct. 13–14	439	41.7	7 622	14 610	18 229	80.1
Oct. 27	329	11.9	941	6 676	7 771	(85.9)
Nov. 9	321	13.7	1 186	3 167	8 494	37.3
			Monthly catch			
			Investigated C	Total		
1978						
Sept. 7	492	42.9	35 857	53 108	83 387	63.7
Sept. 27	200	62.5	37 590	53 108	59 967	88.7
			Monthly Catch C			
Bead marks						
1978						
Sept. 27	200	83.0		53 108	63 929	83.1
Oct. 11	400	77		77 066	100 012	77.1
Oct. 24	464	38.6		77 066	199 090	38.7

TABLE 5. Results from tagging experiments at the Pyhäjoki River in 1977 and 1978. Total catch from finclipping method recorded as whole catch for September in 1977 and for the time when marked fish were caught in quantity in 1978. For more explanations see Table 4.

Date	Number marked M	Recaptured %	Investigated catch C	Total catch	N'	u (%)
Finclipping						
Sept. 14, 1977	342	8.8	11 535	83 659	127 640	65.5
Sept. 14, 1978	300	37.0	2 134	3 699	5 738	64.5
Bead marks				C		
Oct. 7, 1977	206	53.4		71 671	133 659	53.6
Oct. 21, 1977	212	28.3		71 671	250 262	28.6
Oct. 27, 1977	136	36.8		71 671	192 531	37.2
Nov. 8, 1977	223	10.3		18 450	172 209	10.7
Sept. 25–28, 1978	405	42.5		47 952	112 539	42.6
Oct. 5, 1978	237	59.1		40 093	67 676	59.2
Oct. 11, 1978	176	47.2		40 093	84 484	47.5
Nov. 7, 1978	237	10.1		1 675	15 955	10.5

comparison of daily catches was, however, useful at that time. At the end of October, in the tagging experiment, the proportion of the total catch that was investigated was small (1/7); consequently the bias in the sample multiplies to yield a high approximation of the rate of exploitation.

At Pyhäjoki (Table 5), bead marking began in 1977. A detailed investigation of the daily catch could not be arranged, partly because of the large size of the catch compared to the Kalajoki. In September 1978, however, the finclipping method was tried there (Table 5) with good results. However, in 1977 only one in seven fish was examined for its finclips. This means that the result could be biased even though the estimated rate of exploitation is the same, 64–65% for both years in the middle of September.

Tagging by both methods (finclipping and bead marking) at the same time was tried both in 1977 and 1978 at Pyhäjoki. In both years, however, the investigation of finclipped fish in the catch was not sufficient (7–25% of the catch), and finclipping gave biased results. Bead marking gave a rate of exploitation between 50 and 60% inclusive at the beginning of October. After that the numbers tended to decrease, depending on ice conditions. In both years fishing was practically finished in the first half of November. Only 10% of the upstream migrants were caught at that time.

POPULATIONS

The monthly rates of exploitation and catches were used to calculate the size of the populations of upstream migrants (Tables 6 and 7). It can be seen that the September and October figures are reasonably constant in both rivers. In November when fishing ceased because of the ice, the relevant information obtained from the commercial fisheries was small. As a result, great variation is seen in the estimated numbers running upstream in November especially in the Pyhäjoki, from 173 000 in 1977 to 14 000 in 1978. Thus the November migration, although represented in Tables 6 and 7, must be more or less neglected if populations are compared between rivers and years. Some migration occurs in December also. In the Pyhäjoki River the number running upstream until the end of October was estimated to be about 325 000 in 1977, but this was only half of that in 1978. The November migrants may have increased the total number in 1977 up to 500 000. In the Kalajoki River, the estimated population increased in 1977 by some 10%. However, the total figure 200–230 000 remained low in 1977 and 1978 too when compared with the catches before 1976 (Table 1).

TABLE 6. Calculated upstream migrant population in the Kalajoki River in 1977 and 1978. The rate of exploitation percentages according to tagging experiments.

Month	Monthly catch (C)	Monthly u, %	N'
1977			
Aug.	3 700	65 (used)	5 700
Sept.	44 500	73.7	60 380
Oct.	69 300	80.1	86 517
Nov.	16 200	37.3	43 432
Dec.	300	5 (used)	6 000
	134 000		202 029
1978			
Aug.	2 500	64 (used)	3 906
Sept.	53 000	78.5	67 516
Oct.	77 000	57.9	132 988
Nov.	1 200	5 (used)	24 000
	133 700		228 410

TABLE 7. Calculated upstream migrant population in the Pyhäjoki River in 1977 and 1978. Fishing mortality percentages according to tagging experiments.

Month	Monthly catch (*C*)	Monthly *u*, %	*N'*
1977			
Aug.	11 000	60 (used)	18 000
Sept.	83 500	65.5	127 481
Oct.	71 500	39.8	179 648
Nov.	18 500	10.7	172 897
	184 500		498 026
1978			
Aug.	3 500	60 (used)	6 000
Sept.	48 000	64.5	74 419
Oct.	40 000	53.4	74 991
Nov.	1 500	10.5	14 286
	93 000		169 696

CHANGES IN MIGRATION BETWEEN RIVERS

It is difficult to speak accurately about individual river populations because there is often a great deal of movement of lampreys from their native river into neighboring rivers. This seems to be connected with changes in the quality of river waters. The best evidence for this has been obtained from the southern neighboring rivers, Kalajoki and Lestijoki. Also, I believe that a rapid decrease in the number of lampreys in the Pyhäjoki River in 1978 was caused by disturbances in the Pyhäjoki catchment area, where intensive construction work and dredging in the upper courses was being carried out in the autumn of 1978.

In the Lestijoki River the water quality was exceptionally poor in the autumn of 1978 and the lamprey catch decreased to one third of "normal" and was an even smaller proportion of the excellent catch in 1976. Water analyses by the National Water Board, in the Kokkola district, showed exceptionally high nitrate concentrations in the river in September 1978, the origin of which was a cheese factory. However, later evidence indicated that acute changes in pH from the same source are responsible for the main disaster. Most of this kind of wastewater and domestic sewage was run practically unpurified through a new wastewater treatment plant alongside the river, which was still not in full operation. As a result, ammocoetes moved out of the river mouth, and many dead perch (*Perca fluviatilis*) and young brown trout (*Salmo trutta*) were found in the river. Untreated domestic sewage was discharged throughout the autumn at the normal time of the lamprey migration.

Tagging experiments were unsuccessful in demonstrating movement between the rivers in the autumn of 1978. One finclipping experiment was carried out in the Lestijoki in the middle of September 1978 with an unusually low recapture of 37%, but these lampreys couldn't be identified from neighboring rivers. Another tagging trial was carried out at the beginning of November using bead marks. Three hundred tagged lampreys were put into the sea at the coast about 5 km north from the river mouth (which is in the direction of the present main study rivers). Only some tagged fish were recaptured, however, because of the cessation of fishing. Altogether three tagged fish were captured from the Kalajoki, 2 from the Pyhäjoki, and 30 (10%) from the Lestijoki. The fishing season ended at the same time in all of the rivers.

In the autumn of 1976, when the catch in the Kalajoki was much reduced, the catch in the Lestijoki was exceptionally good, over 200 000 lampreys. In 1976 the Hautaperä basin in the Kalajoki was completed and filled with water so that the first discharge began in December 1975. The most extensive work since 1972 was carried out in the Kalajoki in the winter of 1976 (Kilpinen 1979).

Normal values for O_2, P, Fe, and solids in the river water were found in the autumn, unlike the previous winter (Kilpinen 1979). The iron concentration was about 2 mg/L which had become a rather constant value in the river during the 1970s.

Lampreys tagged from the Kalajoki or Pyhäjoki runs were released into the same river mouths from which they were captured. Different bead colors were used in each river. Of 1064 lampreys tagged at the Kalajoki in 1978, two were found in the Pyhäjoki and one in the Perhojoki, south of the Lestijoki. Of 1055 lampreys tagged at the Pyhäjoki in 1978, two were recaptured at the Kalajoki, one in the Kemijoki in 1979. However, the results show only that lampreys can return to the sea and migrate over long distances there — in this case about 200 km. In 1977, when bead marks were used only in the Pyhäjoki, three tagged fish were recaptured in the Kalajoki.

Discussion

Good areas of production of ammocoetes are restricted to the lower courses of the rivers, due primarily to the hydroelectric dams and also to the presence of rapids. As in the case of the Lestijoki, fairly good populations of upstream migrants have been counted even in rivers with a mean discharge of only about 10 $m^3 \cdot s^{-1}$ (Table 8). On the Swedish side of Bothnian Bay (Asplund and Södergren 1974), 15 km of open undammed river was sufficient to maintain a population of over 200 000 individuals. Areas of good larval production may occur even 40–45 km from the river mouth (Salmela 1978; Kainua and Valtonen 1980) and the proportionally larger production area seems to allow a genuine increase in numbers (Table 8). The effective upstream area for larval production has not been established for all open rivers in Finland.

However, changes in the quality of the river water may lead to lampreys moving to a river other than their

TABLE 8. Mean discharge of water, length of river open to larval production, and estimated populations of migrating lampreys in certain rivers running into Bothnian Bay.

River	Mean discharge, $m^3 \cdot s^{-1}$	Main (open) area of larval production, km of river	Population N'	References
Rickleå	13.2	15	194–224 000	Asplund and Södergren 1974
Lestijoki	11.4	30	~500 000	Valtonen and Niemi 1979; additional material
Kalajoki	35.6	40 (main area)	200–800 000	This study
Pyhäjoki	30.8	20 (main area)	400–500 000	Tuunainen et al. (1980); this study

native one. It is also possible that a large river with a strong discharge can attract a large number of migrating lampreys from neighboring small rivers.

Tagging experiments carried out at the Kalajoki River at the beginning of September showed lower recapture rates than those at the end of September, although fishing efficiency was practically unchanged. The main reason for the difference seems to be the behavior of the lampreys, which migrate less strongly earlier in the year than they do later in autumn, so that more may return to the sea during the initial migrations. Evidence of such behavior is also available from the tagging data of Tuunainen et al. (1980), which reveal definite movements between the rivers examined in the present study. It is possible that the lampreys have erroneously entered some river other than that of their origin and that they then return to search for their native river. If this is so, tagging results from the middle and end of September ought to indicate some cumulative effect from previous taggings, as shown by Asplund and Södergren (1974) on the opposite side of the Bothnian Bay where about 5% tagged lamprey was recaptured more than 1 week after being released.

ASPLUND, C., AND S. SÖDERGREN. 1974. Flodnejonögats (*Lampetra fluviatilis* L.) lekvandering i Rickleån. Zool. Revy 36: 111–119.

KAINUA, K., AND T. VALTONEN. 1980. Distribution and abundance of European river lamprey (*Lampetra fluviatilis*) larvae in three rivers running into Bothnian Bay, Finland. Can. J. Fish. Aquat. Sci. 37: 1960–1966.

KLAPURI, K. 1972. Kalastuksesta ja kalan markkinoinnista erityisesti eteläisen Perämeren alueella. [Fishing and fish marketing in the southern Bothnian Bay area. M.Sc. thesis.] Maatalouspolitiikan laitos, Helsingin yliopisto. 321 p. + 72 fig. and tables.

KILPINEN, I. 1979. Vesistötöiden työnaikaisesta vaikutuksesta veden laatuun Kalajoen vesistössä. [Effect of water construction works on the water quality in the Kalajoki river.] Diplomityö XIII + 79 p. + 40 fig. and tables. Oulun yliopisto, Rakentamistekniikan osasto.

RICKER. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

SALMELA, R. 1978. Perhojoen keskiosan järviyhtymän säännöstelyhankkeen kalataloudellisista vaikutuksista. [Effect of the regulation of the water level in the lake area of the central Perhojoki River on fisheries.] Duplicate; 99 p. Vesihallitus.

TUUNAINEN, P., E. IKONEN, AND H. AUVINEN. 1980. Lampreys and lamprey fisheries in Finland. Can. J. Fish. Aquat. Sci. 37: 1953–1959.

VALTONEN, T., AND A. NIEMI. 1979. The present state of fishing in Lestijoki, a small river in Finland. Int. Ver. Theor. Angew. Limnol. Verh. 20: 2085–2091.

Ecology of the European River Lamprey (*Lampetra fluviatilis*) in Northern Sweden[1]

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SJÖBERG, K. 1980. Ecology of the European river lamprey (*Lampetra fluviatilis*) in northern Sweden. Can. J. Fish. Aquat. Sci. 37: 1974–1980.

River lamprey is widely distributed along most of the Swedish coast and is the basis for a number of fisheries. The length of larval life in the river is uncertain. Metamorphosed lampreys (mean length: 105 mm) move downstream at night, mainly during March to May. The upstream spawning run of adults from the sea starts in August and continues for many months. During this migration large numbers of lampreys are caught in traps by fishermen. Spawning takes place in late May or early June when the water temperature reaches about 10°C. Adult lampreys have several predators in the river, especially certain birds (goosander, *Mergus merganser*) and fish (burbot, *Lota lota*).

Key words: lamprey, Sweden, fishery, larvae, metamorphosis, age, length, spawning, predators, migration

SJÖBERG, K. 1980. Ecology of the European river lamprey (*Lampetra fluviatilis*) in northern Sweden. Can. J. Fish. Aquat. Sci. 37: 1974–1980.

La lamproie fluviatile européenne est largement répandue le long de la plus grande partie de la côte suédoise et est la base de plusieurs pêcheries. On n'est pas sûr de la durée de la vie larvaire en rivière. Les lamproies métamorphosées (longueur moyenne : 105 mm) se déplacent en aval la nuit, surtout de mars à mai. La migration de ponte des adultes de la mer vers l'amont débute en août et se poursuit pendant plusieurs mois. C'est l'époque à laquelle un grande nombre de lamproies sont capturées dans des trappes tendues par les pêcheurs. La ponte a lieu fin mai ou début juin quand la température de l'eau atteint environ 10°C. Les lamproies adultes ont plusieurs ennemis en rivière, surtout certains oiseaux (le harle commun, *Mergus merganser*) et poissons (la lotte, *Lota lota*).

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FISHING for the European river lamprey (*Lampetra fluviatilis*) in northern Sweden is mentioned in the literature and in official reports as long ago as the 15th century. From the middle of the 16th century it is noted in tax registers, and Linnaeus mentions it in the account of his journey to northern Sweden in 1732 (von Platen and von Sydow 1975). Although this fishing, up to recent times, has been quite important locally, there are very few direct studies on the ecology of lampreys in Sweden. Much more attention has been given to Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), grayling (*Thymallus thymallus*), and whitefish (*Coregonus* spp.), which are usually found in the same rivers as lampreys.

However, the general biology of river lamprey in the Rickleå River, a medium-sized river in northern Sweden, has been described by Asplund and Södergren (1975) and Sjöberg (1975). Asplund and Södergren (1975) also calculated the population size of lampreys in the same river. Lindroth (1954) and Fogelin (1972) described the downstream drift of ammocoetes and metamorphosed larvae of river lamprey. Hagelin and Steffner (1958) and Hagelin (1959) gave detailed descriptions of the spawning behavior of river lamprey in aquarium experiments.

The fishing methods for river lampreys are described in detail in the literature. From the southernmost of the lamprey rivers of importance in Sweden, the Dalälven River, Ehn (1970) recorded the fishing procedure and handling of the animals. From rivers further north, mainly the Rickleå River, a comparable account is given by Sjöberg (1980), while Storå (1978) has covered lamprey fishing practices over the whole Bothnian Bay area.

European brook lamprey (*Lampetra planeri*) was studied by Enequist (1937), who also discussed the taxonomy of river lamprey and brook lamprey. The latter species has also been studied in the southernmost

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part of Sweden by Malmqvist (1978). Only one paper (Nybelin 1979) describes details of the ecology of the Atlantic sea lamprey (*Petromyzon marinus*), an uncommon species in Sweden.

The aim of this study is to review present knowledge of the ecology of river lamprey in Sweden, and is based both on literature studies and on personal investigations. Most of the data are from the Ricklea River in the province of Västerbotten in northern Sweden.

Study Area

Along the northern Swedish coast a large number of rivers run into the sea southeastwards, one of them being the Rickleå River. It is a medium-sized watershed with most of its catchment area within the northern coniferous belt of the Taiga region. The river has a length of 48 km from its mouth in the Gulf of Bothnia at 64°10′N, to its origin in the Bygdeträsket Lake, which has an area of 29 km^2.

Although the Rickleå River flows mainly through coniferous forests, the forest close to the shores is sometimes interspersed with a belt of agricultural land, which broadens towards the coastal area. Granite gneisses dominate in the lower parts of the basin.

Anadromous fish can penetrate the river up to 15 km from the mouth, where a series of hydroelectric dams stop further migration. The difference in height between sea level and the dams is about 40 m. Along the stretch of 15 km are 17 rapids which constitute 3.8 km, or 25% of this part of the river. The rapids are generally 20–30 m wide and 0.5–2 m deep, while the slow-flowing parts are 30–50 m wide and 2–3.5 m deep at mean water levels (Karlström 1978).

The mean water discharge is 16 $m^3 \cdot s^{-1}$, but there are large fluctuations throughout the year. Normally there are two major peaks. The larger one, the spring discharge, has its maximum during May and is estimated to be 160–180 $m^3 \cdot s^{-1}$, while the summer values range from 3 to 10 $m^3 \cdot s^{-1}$. Besides the spring peak there is often a second, smaller peak caused by the autumn rains. The annual water level amplitude is about 1.5 m. After a spring flood drop, the pH stabilizes at around 6.4–6.5 during the summer (Karlström 1978). Temperature of the water reaches 20–30°C in July and August. Ice covers the slow-flowing sections from the middle of November to the end of April or the beginning of May.

According to Södergren (1976), 19 fish species are found in the river.

Methods

Ammocoete larvae were collected by digging along the edges of those stretches of the river where lampreys were known or supposed to have their breeding grounds. Sand or gravel down to a depth of about 1 dm was washed through a sieve.

Newly metamorphosed river lampreys were caught in a plankton net in May and June during the downstream drift. After anaesthetization in MS 222, the length of each animal was measured to the nearest millimetre.

Results

DISTRIBUTION

In Sweden the river lamprey occurs along the entire coast, although it is common only in the northern coastal regions (Lilljeborg 1891). In the official Swedish fishery statistics, figures for lamprey catches are given only for the Dalälven River, about 100 km north of Stockholm, and for rivers further north. The only exception is from the southeastern province of Kalmar, where small numbers of lampreys were caught in the 1910's. From the Dalälven River and northwards, however, the river lamprey is most likely to be present in all the larger watersheds up to the northern river bordering Finland, the Torne River. Sjöberg (1980) presents details from 15 rivers along this coastline of the fishing activities which occur today or occurred up to the date of the building of hydroelectric dams.

Most of the fishing grounds are close to the mouth of the rivers concerned. However, where the lampreys are not stopped by dams, they can penetrate the river for fairly long distances. In the Ångermanälven River, for example, one fishery is located about 150 km upstream.

Information on the distribution of river lamprey in the sea after the metamorphosed lampreys have left the rivers is very sparse. Lampreys are now and then caught accidentally by fishermen netting herring during summer and autumn. Widegren (1861) discusses a fishery in the province of Norrbotten and notes that lampreys are present in large numbers in the archipelago. During the summer they follow herring and attach themselves to this species. He notes further that such herring were caught daily during the summer in the northernmost part of Bothnian Bay. There do not appear to be any other Swedish references concerning the occurrence of river lamprey in the sea.

Brook lamprey is distributed all over the country with the exception of the northwest (Curry-Lindahl 1961). In the Rickleå River it is found in small numbers (Malmqvist 1978).

Sea lamprey was found on one occasion in the Rickleå River (July 19, 1965) (Lars Österdahl, University of Umeå, personal communication). One specimen was caught in a salmon trap, which was in operation close to the mouth of the river from the end of May to the end of October 1961–67. This species is never found by local fishermen, who fish for river lampreys during the autumn.

AMMOCOETES AND METAMORPHOSED LARVAE

Information on downstream drift of ammocoetes and newly metamorphosed lampreys in Swedish rivers are given for the Indalsälven River by Lindroth (1954,

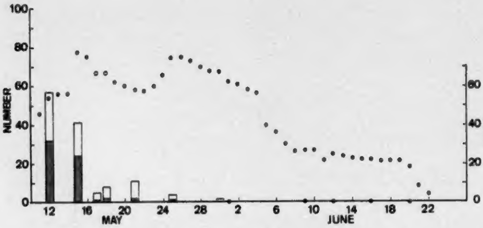

FIG. 1. Number of ammocoetes (□) and metamorphosed larvae (▨) of the river lamprey caught in a plankton trap during 2-h periods (22–24 h). Open circles indicate changes in water level (cm) during the investigation period.

1957) and by Fogelin (1972). They both concluded that ammocoetes drift downstream in spring and that this drift is nocturnal.

Different writers have assumed that movements towards the estuaries takes place in the period between late winter and early summer (e.g. Enequist 1937; Bahr 1952; Hardisty et al. 1970). In the Rickleå River, Fogelin (1972) found newly metamorphosed river lampreys migrating downstream at the beginning of May, and he suggested that this was the end of the migration period. The period before the start of Fogelin's investigation was covered by Södergren (University of Umeå, personal communication), who had a drift trap operating from January up to a spring flood at the beginning of May. He obtained metamorphosed lampreys from the middle of March up to the beginning of May. Fogelin's (1972) assumption that the drift in May reflected the end of the downstream migration is verified in my present study (Fig. 1), where the migration during the spring flood was studied by the use of a plankton net trap placed in the middle of the stream. The same migration pattern as found by Fogelin (1972) was repeated.

Starting on May 12, the trap caught metamorphosed lampreys for the first few nights, and for a short period thereafter (Fig. 1). No lampreys were caught during the day. It is assumed therefore that the downstream migration of metamorphosed lampreys in the Rickleå River occurs from the middle of March to the middle of May mainly during the night. These results agree with those of Hardisty and Potter (1971a) from British rivers. The lengths of the metamorphosed lampreys ranged from 90 to 127 mm while the mean length of the total sample of 82 specimens was 105 mm. Ammocoetes were also caught in the same trap. Even these drifted during the night (Tables 1 and 2), but the numbers did not decrease so abruptly during the season as did those of metamorphosed lampreys (Fig. 1).

It is not possible to determine exactly the number of year-classes among the larvae from the drifted ammocoetes, even including larvae collected from silt beds in the river. However, although the sample size is small, the figures at least do not contradict the proposition that in the Rickleå River the larvae live for at least 5 yr before transformation. The sex of the larvae was not determined. Malmqvist (1978) found differences in number of year-classes of brook lamprey from different small rivers in southern Sweden, even when the distance between them was small. He also found differences between male and female larvae.

SPAWNING RUN

In the Rickleå River the spawning run starts in August and continues throughout the year. Most of the fishing is carried out in the rapids within 1 km from the mouth of the river, and the main fishing period is during September, October, and November. Lampreys are caught mainly in wooden traps placed between stones at the bottom of the rapids (Sjöberg 1980). Lampreys caught during the beginning of the run have greater mean lengths and weights than those

TABLE 1. Occurrence of ammocoetes caught accidentally in fish traps in the Rickleå River during 24-h periods from June to September, 1974 and 1976. No animals were caught in June or July.

Time of day	August				September				
	03–04	06–07	07–08	08–09	03–04	04–05	12–13	17–18	24–25
12–14									
14–16									
16–18									
18–20								1	1
20–22								1	
22–24			1	1	1	1		1	
00–02	1			1		1			
02–04				1					
04–06									
06–08									
08–10									
10–12									

TABLE 2. Numbers of ammocoetes and of metamorphosed larvae of river lamprey caught in a plankton trap in the Rickleå River for 3 d in May 1979.

Date	Time	Ammocoetes	Metamorphosed larvae
May 12	22:00–24:00	22	32
May 13	11:30–12:30	0	0
May 15	22:00–24:00	17	24

caught later on (Asplund and Södergren 1975; Sjöberg 1975). The mean values of weight and length from the Rickleå River are small compared with figures given by, for example, Lanzing (1959) from the river Maas in the Netherlands. A trend of decreasing mean values from north to south and even from east to west is pointed out by many writers, e.g. Lanzing (1959) and Asplund and Södergren (1975).

During the spawning run the lampreys are caught at night. The traps are put out in the evening and are taken up in the morning. The nocturnal behavior of lampreys during the autumn has been experimentally demonstrated by Wikgren (1954) (see also Tesch 1967). According to the fishermen, the catch is very dependent on weather conditions. Dark, rainy nights without moonlight and with a wind resulting in a high sea level are said to give the best results. These beliefs, with slight variations, are shared among fishermen over a large geographical area and are old-established. Selegio (1926) reports the same opinion from Dvina, and Juvelius (1772) referred to almost exactly the same experiences as long as 200 yr ago. Asplund and Södergren (1975) have statistically verified the positive correlation between a good catch and dark nights (see also Tesch 1967).

In early spring, before ice has gone from the river, the lampreys are apparently quite inactive and very few are caught (Fig. 2). However, as soon as the ice has gone at the end of April or early May, the water temperature rises, and in May there is often a peak in the number of lampreys caught (Fig. 2). Whether this peak is caused by an extra spawning run, as is described from the Neva by Ivanova-Berg (1936), or is caused by local movements of overwintering animals, is not known.

SPAWNING

Spawning starts at the beginning of June or the end of May when the water temperature is about 10°C (Sjöberg 1977). From having been strictly nocturnal, the lampreys now are active during both day and night. This 24-h activity seems to be caused by the addition of diurnal behavior to the basic nocturnal behavior, and does not seem to be caused by the light nights at this latitude during the midsummer period (Sjöberg 1977).

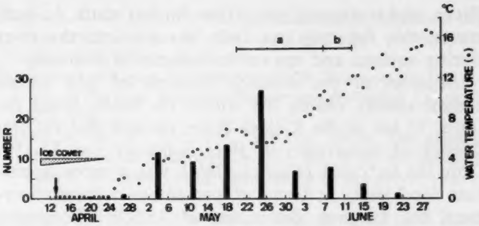

FIG. 2. Seven-day means of the numbers of river lampreys caught in a lamprey trap in the Rickleå River, 1972. Water temperatures are indicated by closed circles. (a) Development of secondary sexual characters; (b) spawning. Arrow indicates start of investigation.

PREDATION

In spring, the river lamprey is the most important food item for the goosander (*Mergus merganser*), which is quite a common bird in the coastal areas of all the northern Swedish rivers. These birds utilize the lamprey for food as soon as there are openings in the ice (which are associated with rapids in the river) through which they can dive for fish. River lampreys made up 23% of the wet weight of the contents of 19 goosander stomachs (and occurred in 16%) collected from the Rickleå River (Sjöberg 1974). Red-breasted mergansers (*Mergus serrator*) also feed on the river lamprey, but probably to a lesser extent, partly because they arrive later in the season and are present in lower numbers on the river. They also seem to choose smaller food items. Although goosanders feed on the river lamprey, there are not sufficient numbers of these birds to be important in controlling lamprey populations. Also they are present in the river for a relatively short part of the year. The main period of predation is after the fishermen have taken their catch during the autumn.

Even gulls (*Larus fuscus*, *L. argentatus*, *L. canus*) take lampreys to some extent. Their predation on lampreys is mainly during the spawning period. The birds circle over the water surface and snap lampreys that are swimming close to the surface or drifting more or less passively downstream after spawning. This predation takes place mostly during the dark period of each 24 h, and is probably caused by the nocturnal behavior of the lampreys. They are more active in the surface water during the night than during the day (Sjöberg 1975). Thus, it is easier to catch them during the night, in spite of the reduced light conditions. However, the nights are bright enough during this part of the year in these northern latitudes for predation by animals that are normally diurnal.

Another predator on the river lamprey is the burbot (*Lota lota*), which is a common fish in the Rickleå River. There are no figures for the total populations, but Bengtsson (1973) has estimated a spawning population of 7000 individuals in the Sävar River which has a catchment of somewhat smaller size than the Rickleå

River, and is situated just 30 km further south. In both rivers, this fish migrates from the sea into the river during autumn and spawns in January or February.

Analyses of the stomach contents of 244 burbot caught mainly during the winter on hooks along the lower 15 km of the Rickleå River showed that the frequency of occurrence of river lampreys was 11.1%. Only the bullhead (*Cottus gobio*) was a more important food item. In terms of percentage volume, however, the lamprey dominated at 13.9% (Bengtsson 1973).

TOTAL CATCH AND YEARLY FLUCTUATIONS

The Swedish fishery statistics on lamprey fishing cover the years 1914–23 and from 1937 up to the present. The yearly total catch ranged during this period from 4774 to 27 300 kg. Large variations partly depend upon differences in the number of rivers involved. For example, the lamprey catch from the northernmost county of Sweden, Norrbotten, was included in the totals during the period 1914–23 but not later on, though the figures from these rivers are probably low (compare Sjöberg 1980). During 1937 to 1977, the large lamprey catches from the Umeå River are only available from 1952 to 1969, and during this period a large hydroelectric dam was constructed, with an extensive impact on fishing and fishing rights. Many rivers with a good or fairly good lamprey fishery are not included at all, or only occasionally. A good example is the Skellefteå River which, until the building of power stations, had an important fishery. The same is true for the Öre River and Rickleå River, which even now have reasonable fisheries. As noted above, none of the rivers in the province of Norrbotten, including such big rivers as the Kalix and the Torne rivers, are included in the statistics. Thus, the data presented here can only be regarded as minimum values, and the true figures are probably much higher.

Because of these differences in the statistical material itself, it is not possible to make reliable comparisons of the fluctuations from year to year in the lamprey catches. It is more useful to compare catches from the same river. The longest series of data on lamprey catches are from the Dalälven River and the Ljungan River. From these rivers it is evident that there are great fluctuations in catches even in the same river from year to year (Fig. 3). This is especially pronounced in the statistics from the important fishery in the Dalälven River, where peak catches occur at intervals of about 6–8 yr. This is in agreement with the figures presented by Abakumov (1956), which have a 7- to 9-yr cycle. It is also in agreement with data from the Kemi River in Northern Finland (Hurme 1962; Fig. 4).

Although there is not complete agreement, the peaks in the Dalälven and Ljungan rivers usually occur at the same times (Fig. 3). In the Dalälven River there are peaks in 1945 and 1953, i.e. the same given by Abakumov (1956) as peak years in the Gauya River in the Gulf of Riga.

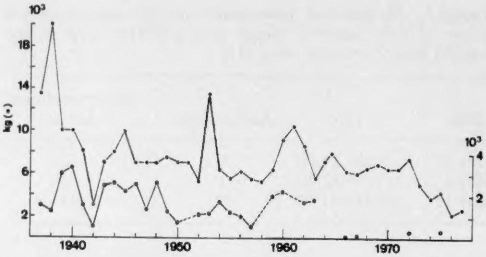

FIG. 3. Yearly catches of river lampreys in the Dalälven River (closed circles) and the Ljungan River (open circles) (data from Official Statistics of Sweden; 1917–23, 1937–77).

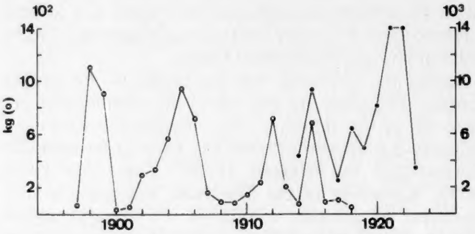

FIG. 4. Yearly catches of river lampreys in the Kemi River (open circles) (from Hurme 1962) and from the Dalälven River (closed circles).

Discussion

Ecology of river lamprey in the rivers of northern Sweden is similar to that reported from other places as regards the autumn migration, spawning, and the downstream drift of ammocoetes and metamorphosed larvae. The duration of the larval stage in the rivers is not known exactly, but present figures support the suggestion of a lifespan in the river of about 5 yr (compare Koli 1975). As is the case for other geographical areas, the adult life in the sea is the least known part of the life cycle since no such investigations have been reported from Sweden. The only information given in the literature is that lampreys are often caught during the summer in nets used for herring fishing; however, the duration of the sea phase is not known.

The ammocoetes and metamorphosed larvae caught in the Ricklea River were captured just downstream from the last of a series of rapids in the river and only 500 m from its mouth. This means that many ammocoetes must be swept out of the river into the estuary. The downstream movement is apparently at least partly a result of an active movement, the reason for which could be redistribution to better living grounds (Hardisty and Potter 1971b). Fogelin (1972) makes the assumption that this downstream movement could be an effect of self-regulation of lamprey population levels. From this point of view, it is interesting to consider the effect of the predation by mergansers and burbot (amounting to a few thousand of lampreys) documented from the Rickleå River. This takes place mostly after the fishermen have removed about 100 000 lampreys during the autumn. However, the breeding population is apparently still capable of producing such large numbers of larvae that the carrying capacity of the river seems to be fully utilized, and a "surplus" of several thousand larvae is swept out of the river.

In the Swedish rivers investigated, there does not seem to be any correlation between the lamprey catch and the salmon catch as was found by Abakumov (1956) in the Gulf of Riga. In the Dalälven River there seems to be a negative correlation between peak years for lampreys and for salmon. Because of the frequent appearance of lamprey marks on herring (reported by fishermen from the northern part of the Baltic during autumn), there ought to be a correlation between the numbers of lamprey and of herring. However, although the catch of herring is perhaps not the best measurement of the numbers of fish in the sea, there is no relationship apparent between the catches of herring and river lamprey.

Acknowledgments

I thank Eric Andersson, Göte Andersson, and Olof Sandström for collecting both lampreys and their prey species and for discussing certain aspects of lamprey ecology. I also thank Sam Södergren and Lars Österdahl for allowing me to use unpublished data from the Rickleå River and Peter Maitland for improving the language of this paper. Parts of this investigation have been supported financially by the Swedish Natural Science Research Council, the Swedish State Power Board, and the University of Umeå.

Asplund, C., and S. Södergren. 1975. Flodnejonögats (*Lampetra fluviatilis* L.) lekvandring i Rickleån. Zool. Revy 36: 111–119.

Abakumov, V. A. 1956. The mode of life of the Baltic river lamprey. J. Vop. Ikhtiol. 16: 133–138. (In Russian) Cited in M. W. Hardisty and I. C. Potter. [ed.] The biology of lampreys. Vol. 1. 1971.

Bahr, K. 1952. Beiträge zur Biologie des Flussneunauges, *Petromyzon fluviatilis* L. (Lebensraum und Ernährung). Zool. Jahrb. Abt. Oekol. Geogr. Tiere Syst. 81: 408–436.

Bengtsson, B. 1973. Ekologiska studier på lake (*Lota lota* L.). Report from Rickleå Field Station 48: 153 p. (In Swedish)

Curry-Lindahl, K. 1961. Fiskarna i färg. Stockholm 1961. (In Swedish) 230 p.

Ehn, W. 1970. Nejonögonfiske i Älvkarleby. Svenka Landsmål Svenkt Folkliv 93: 9–25. (In Swedish)

Enequist, P. 1937. Das Bachneunauge als ökologische Modifikation des Flussneunagues. Über die Fluss- und Bachneunaugen Schwedens. Ark. Zool. 29: 1–22.

Fogelin, P. 1972. Studier över drift av larver och nymetamorfoserade ungar av flodnejonöga (*Lampetra fluviatilis* L.) i Indalsälven och Rickleån. Report from Rickleå Field Station 20: 28 p.

Hagelin, L.-O. 1959. Further aquarium observations on the spawning habits of the river lamprey (*Petromyzon fluviatilis*). Oikos 10: 50–64.

Hagelin, L.-O., and N. Steffner. 1958. Notes on the spawning of the river lamprey (*Petromyzon fluviatilis*). Oikos 9: 221–238.

Hardisty, M. W., and I. C. Potter. 1971a. The general biology of adult lampreys, p. 127–206. *In* M. W. Hardisty and I. C. Potter. [ed.] The biology of lampreys. Vol. 1. 1971.

1971b. The behaviour, ecology and growth of larval lampreys, p. 85–125. *In* M. W. Hardisty and I. C. Potter. [ed.] The biology of lampreys. Vol. 1. 1971.

Hardisty, M. W., I. C. Potter, and R. Sturge. 1970. A comparison of the metamorphosing and macrophtalmia stages of the lampreys *Lampetra fluviatilis* and *L. planeri*. J. Zool. (London) 162: 383–400.

Hurme, S. 1962. The anadromous fishes in the Baltic-side rivers in Finland. Maatalous-hallituksen Kalataloudellinen Tutkinustoimisto. Monistettuja julkaisuja 24: 137 p. (In Finnish with English summary)

Ivanova-Berg, M. M. 1936. Spring migration and spawning of the Neva lamprey. Izv. Akad. Nauk SSSR 1936: 599–604. (In Russian with English summary)

Juvelius, E. 1772. Om Nejnögons Fisket i Österbotten. Tidn. Utgifne Af et Sällskapi Åbo 1772: 158–160, 161–165. (In Swedish)

Karlström, U. 1978. Environmental factors, detritus and bottom fauna in the Rickleån — a North Swedish forest river. Ph.D. thesis, Univ. Uppsala, Sweden. 74 p.

Koli, L. 1975. Retkeilijän kalaopas. Keuruu. 127 p. (In Finnish)

Lanzing, W. J. R. 1959. Studies on the river lamprey, *Lampetra fluviatilis*, during its anadromous migration. Ph.D. thesis, Uitsgeversmaatschappij, Neerlandia, Utrecht, Netherlands. 82 p.

Lilljeborg, W. 1891. Sveriges och Norges fauna. Del 3. Fiskarna. Uppsala, Sweden. p. 693–707.

Lindroth, A. 1954. Fiskeförsök i Indalsälvens mynning 1953. Vandringsfiskutredningen. Meddelande 8: 23 p.

1957. A study of the whitefish (*Coregonus*) of the Sundsvall Bay District. Inst. Freshwater Res. Drottningholm 38: 70–108.

Malmqvist, B. 1978. Population structure and biometry of *Lampetra planeri* (Bloch) from three different watersheds in South Sweden. Arch. Hydrobiol. 84: 65–86.

Nybelin, O. 1979. Några iakttagelser över havsnejonögats lek. Fauna Flora 74: 208–213. (In Swedish)

Official Statistics of Sweden. 1917–23, 1937–77. National Central Bureau of Statistics. Stockholm.

von Platen, M., and C. O. von Sydow. 1975. Carl Linnaeus Lapplands resa år 1732. Stockholm, Sweden. (In Swedish)

Selegio, A. 1926. Die Fisherei in den Fliessen, Seen und Strandgewässern Mitteleuropas, p. 1–422. *In* R. Demoll and H. N. Maier [ed.] Handbush der Binnenfischerei Mitteleuropas. Band V. Stuttgart, W. Germany.

Sjöberg, K. 1974. The food of the goosander (*Mergus merganser* L.) in northern Sweden. Report from Rickleå Field Station 52: 12 p.

1975. Spawning period, locomotor activity and length/weight of the river lamprey (*Lampetra fluviatilis* (L.)) in the Rickleå River, province of Västerbotten, Sweden. Zool. Revy 36: 41–47. (In Swedish with English summary)

1977. Locomotor activity of river lamprey *Lampetra* *fluviatilis* (L.) during the spawning season. Hydrobiologia 55: 265–270.

1980. River lamprey fishing in Sweden. Paper presented at "River Ecology Symposium" at Oulu University, Finland, 1977. (In press)

SÖDERGREN, S. 1976. Ecological effects of heavy metal discharge in a salmon river. Rep. Inst. Freshwater Res. Drottningholm 55: 91–131.

STORÅ, N. 1978. Lamprey fishing in the rivers of the Gulf of Bothnia. Ethnol. Scand. 1978: 67–98.

TESCH, F.-W. 1967. Aktivität und Verhalten wandernder *Lampetra fluviatilis*, *Lota lota*, und *Anguilla anguilla* im Tiydegebiet der Elbe. Helgol. wiss. Meeresunters. 16: 92–111.

WIDEGREN, H. 1861. Om fisk-faunan och fiskerierna i Norrbottens län. Reseberättelse Afgiven den 10 mars 1860. Stockholm, Sweden. (In Swedish)

WIKGREN, B.-J. 1954. Dygnsrytmiken hos nejonögat (*Petromyzon fluviatilis* L.) Memoranda Soc. Fauna Flora Fenn. 29: 24–27. (In Swedish with English summary)

Scarring of Whitefish (*Coregonus lavaretus*) by European River Lamprey (*Lampetra fluviatilis*) in Loch Lomond, Scotland[1]

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MAITLAND, P. S. 1980. Scarring of whitefish (*Coregonus lavaretus*) by European river lamprey (*Lampetra fluviatilis*) in Loch Lomond, Scotland. Can. J. Fish. Aquat. Sci. 37: 1981–1988.

Whitefish are abundant in Loch Lomond and have been attacked by lampreys for over 100 yr. In all samples (totalling about 1000 whitefish) taken from different parts of the loch between 1951 and 1979 the incidence of lamprey scarring was high (from 26 to 50%), many times that of any of the other 14 species of fish in the loch. Multiple scarring was common. Small whitefish (less than 25 cm) were rarely scarred, whereas larger ones (more than 25 cm) frequently had been attacked. Scars occurred all the year round, but fresh wounds only in the summer — especially July and August. Almost all the scars occurred along the backs of the fish between the head and adipose fin, and above the lateral line. There is little evidence that these attacks affected the growth or condition of the whitefish concerned. Lampreys do not appear to attack fish in freshwater in other parts of Great Britain, but parasitism has been recorded in a few lakes in Finland and Russia.

Key words: scarring, *Coregonus lavaretus*, *Lampetra fluviatilis*, Scotland

MAITLAND, P. S. 1980. Scarring of whitefish (*Coregonus lavaretus*) by European river lamprey (*Lampetra fluviatilis*) in Loch Lomond, Scotland. Can. J. Fish. Aquat. Sci. 37: 1981–1988.

Le lavaret est abondant dans le loch Lomond et, depuis de 100 ans, est la victime des lamproies. Dans tous les échantillons (environ 1000 lavarets au total) prélevés à différents endroits du loch entre 1951 et 1979, la fréquence des cicatrices de lamproies était élevée (26–50%), plusieurs fois plus élevée que chez les 14 autres espèces de poissons qui habitent le loch. Plusieurs cicatrices se trouvent communément sur un même poisson. Les petits lavarets (de moins de 25 cm) portent rarement des cicatrices, alors que les individus plus grands (de plus de 25 cm) sont fréquemment attaqués. On observe des cicatrices tout au long de l'année, mais on ne voit de blessures fraîches qu'en été — surtout en juillet et août. Presque toutes les cicatrices sont situées sur le dos de l'animal, entre la tête et la nageoire adipeuse, et au-dessus de la ligne latérale. Les données disponibles ne suffisent pas à démontrer que ces attaques affectent la croissance ou la condition du lavaret. Les lamproies ne semblent pas attaquer les poissons en eau dauce dans d'autres parties de la Grande-Bretagne, mais on a signalé des attaques dans quelques lacs de Finlande et de Russie.

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FISH fauna of Loch Lomond (listed in Table 1) has been described by Stuart (1796), Parnell (1838), Brown (1891), Lumsden and Brown (1895), Lamond (1931), Hunter et al. (1959), and Maitland (1972), most of whom mention the presence of both lampreys and whitefish, *Coregonus lavaretus* (known locally as powan), and that the former prey commonly on the latter.

The first clear account of attacks by the European river lamprey, *Lampetra fluviatilis*, on *Coregonus lavaretus* (formerly known as *C. clupeoides*), was given by Robertson (1875), who found dead powan with lamprey bites, and even with living lampreys still attached. Subsequently, Lamond (1922) diagnosed a supposed "disease" of powan as being the wounds resulting from lamprey attacks. Slack (1955) reported that about 17% of powan examined from Loch Lomond showed fresh, or more often, healed lamprey wounds. Though adult lampreys have not been studied in the Loch Lomond area, research on ammocoete larvae was carried out by MacDonald (1959). However, considerable doubt has now been cast on the validity of his results (Potter and Osborne 1975) and they are probably best ignored.

The research on powan initiated by Slack et al. (1957) was continued by the author and expanded to embrace studies of *Coregonus* in other waters (Mait-

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TABLE 1. Check list of fish species known to occur in Loch Lomond.

Species	Common name
Petromyzon marinus Linnaeus, 1758	Sea lamprey
Lampetra fluviatilis (Linnaeus, 1758)	River lamprey
Lampetra planeri (Bloch, 1784)	Brook lamprey
Salmo salar Linnaeus, 1758	Atlantic salmon
Salmo trutta Linnaeus, 1758	Brown trout
Coregonus lavaretus (Linnaeus, 1758)	Whitefish (Powan)
Esox lucius Linnaeus, 1758	Northern pike
Phoxinus phoxinus (Linnaeus, 1758)	Minnow
Rutilus rutilus (Linnaeus, 1758)	Roach
Noemacheilus barbatulus (Linnaeus, 1758)	Stone loach
Anguilla anguilla (Linnaeus, 1758)	Eel
Gasterosteus aculeatus Linnaeus, 1758	Three-spined stickleback
Pungitius pungitius (Linnaeus, 1758)	Ten-spined stickleback
Perca fluviatilis Linnaeus, 1758	Perch
Platichthys flesus (Linnaeus, 1758)	Flounder

land 1966a, 1967a, b, 1969, 1970). During this work the incidence and position of fresh and healed lamprey wounds was recorded for most samples of fish caught. These results form the basis of the present paper which describes the incidence, position, and effect of lamprey scars on powan in Loch Lomond.

STUDY SITE

Detailed descriptions of Loch Lomond (56°05′N, 4°35′W) have been given elsewhere (Lamond 1931; Slack 1957) and only the major features relevant to this study are noted here (Fig. 1). With a surface area of 71 km^2 this loch is the largest single area of freshwater in Great Britain and is also one of the deepest (maximum: 198 m). Its basin has a dual character with a long, narrow, deep, northern trough and a broad, shallow, southern basin within which are found many islands. The catchment area of 769 km^2 is divided (like the loch) by the Highland Boundary Fault; to the north of this much of the land is exposed metamorphic rock, to the south the richer sedimentary rocks have an extensive covering of drift deposits.

The water of Loch Lomond undergoes a full circulation each winter when the bottom temperatures are normally 4–5°C. In severe winters ice may cover the southern basin but never the northern one. Oxygen levels are always high, even under stratified conditions which are common and stable each summer in the northern basin, but transient and unstable in the southern basin. The water is normally very clear (Secchi transparency: 5–6 m) with a pH of 6.6–7.1 and a calcium content of 7–12 mg/L. Chemical conditions are always richer in the southern basin than in the northern.

An extensive system of tributaries drain the catchment and offer nursery areas for ammocoete larvae of the three British species of lamprey — all of which (Table 1) occur in them. The most important is the River Endrick entering the southeast corner of the loch (Maitland 1966b). Five significant tributaries enter the west side of the loch, while the main outflow is the River Leven which is the route of migrating lampreys (as well as other fish species) to and from the sea, and is also a spawning and nursery area.

Methods

Data on the incidence of lamprey scars on powan were collected in various years from 1951 to 1979 at eight netting sites in Loch Lomond (Fig. 1). Some of the fixed stations gillnetted each year are important spawning grounds for powan and produced large samples during the winter months (Maitland 1969). During the summer months, seine-netting was carried out on suitable shores all round the loch and its islands — especially in the southern basin.

Although the main purpose of the work was to study the biology of the powan, lamprey marks occurred so regularly on these fish that their incidence was recorded accurately. This was done by noting the number of fresh or healed wounds on each powan and plotting their position (and whether on the left side or right) on outline diagrams (see Fig. 3). Other species of fish in the loch from some mixed collections were fully examined for lamprey wounds.

In one sample of powan, collected in January 1979, the size (length and breadth in millimetres) of clearly distinguishable lamprey scars was measured.

Apart from specific captures or sightings of lampreys reported in the literature (Lumsden and Brown 1895; Lamond 1922, 1931, etc.), only occasionally are adults seen in the loch, either on their own or attached to fish. Adult river lamprey catches in recent years have occurred during the evening seine-netting for salmon and trout carried out by a local proprietor. Powan occur commonly in these nettings and each season one or more lampreys are seen: occasionally they appear to be relatively common.

Results

INCIDENCE OF LAMPREY SCARS

Of the fish species in Loch Lomond, only the six larger ones (salmon, trout, powan, pike, roach, and

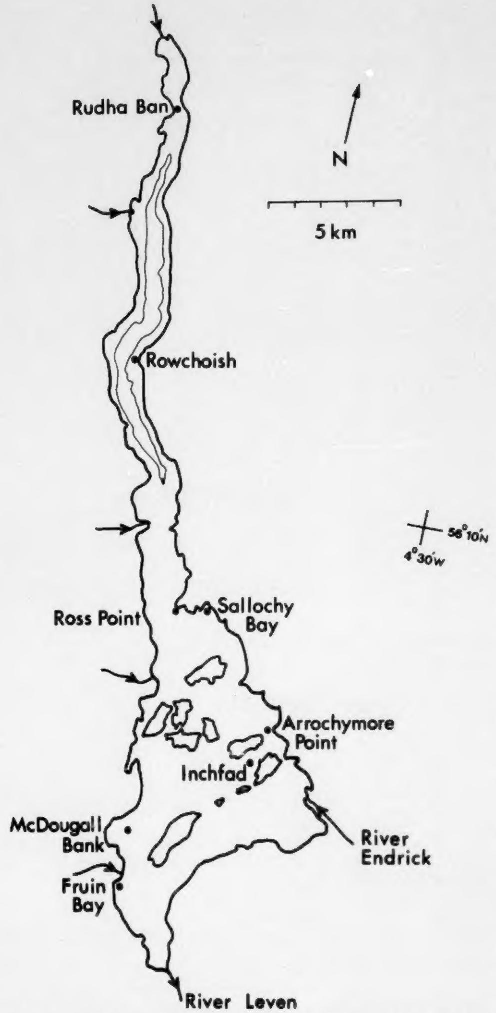

FIG. 1. Loch Lomond, showing the major stations where powan were collected during the present study.

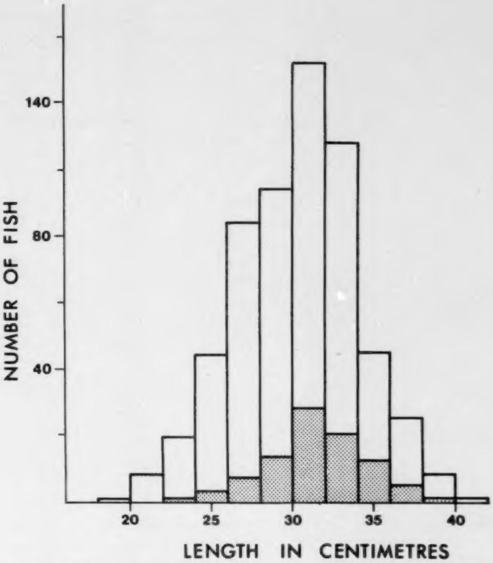

FIG. 2. The length frequency distribution of unscarred (open) and scarred (stippled) powan collected at different places in Loch Lomond in 1966.

perch) were caught regularly enough to be worth examining for scars. The results for 1965–66 showed that three species were being parasitised: trout (6% with scars), powan (45%), and roach (5%). Except for occasional salmon, no wounds were recorded from the other species of fish noted above though many hundreds of each of them have been examined during other studies (Mills 1969; Shafi and Maitland 1971a, b). Salmon occasionally carry lamprey scars, and some adults caught in Loch Lomond bear large scars, possibly caused by the sea lamprey, *Petromyzon marinus*: Lamond (1931) records that a large salmon was actually landed from the loch with a sea lamprey still attached.

The incidence of scarred powan (Table 2) was always high and ranged from 26 to 50% of the total. Many fish bore only one scar but two scars were quite common and multiple scarring with as many as eight independent scars was not unusual. Fifty-five percent of the scarred fish carried more than one scar.

The incidence of scarring in relation to the length of fish was examined for powan collected in 1951 and in 1966 (Fig. 2). Fish below 20 cm are virtually never scarred. (Though the samples presented here are small, many small powan were examined in other parts of the study. These were never found to bear scars.) Fish below 25 cm are rarely scarred, but between 25 and 35 cm scarring is very common and rises well above 50% in some years. Though the number of fish longer than 35 cm examined in both years was small, in both cases the incidence of scarring appears less than in the 25- to 35-cm group.

This paper is concerned almost entirely with healed lamprey wounds (scars) on powan; the actual timing of attacks was not studied in detail. However, field notes from catches at different times of the year indicate that fresh wounds occurred only in the summer months (June to October) whereas scars were present all the year round. In 1979, fresh wounds were common in July and August.

TABLE 2. The incidence of lamprey scars on large samples of powan netted in Loch Lomond (1951–79) and examined specifically for scarring.

Sample details	No. powan	% scarred	Number of scars 1	2	3	4	5	6	7	8
Fruin Bay 1951	105	26	15	8	4	0	0	0	0	0
Inchfad 1952	63	38	20	2	1	0	1	0	0	0
McDougall Bank 1964	70	46	17	8	3	1	0	2	1	0
McDougall Bank 1966	52	44	12	5	3	0	1	2	0	0
Arrochymore Point 1966	111	40	21	9	5	5	3	0	1	0
Rowchoish 1966	74	38	7	7	7	5	1	0	1	0
Rudha Ban 1966	98	43	14	10	8	6	1	0	1	2
Ross Point 1966	132	43	25	17	7	7	1	0	0	0
Ross Point 1967	67	37	9	7	8	0	1	0	0	0
Sallochy Bay 1967	101	50	15	17	6	6	3	1	1	1
Sallochy Bay 1979	102	28	18	5	2	3	0	1	0	0
Totals	975	39	173	95	54	33	12	6	5	3

POSITION OF LAMPREY SCARS

The position and number of lamprey scars were recorded carefully on all the fish listed in Table 2. Based on these data the location of lamprey scars was very consistent, with the great majority occurring along the back of the fish, between the head and the adipose fin, and above the lateral line (Fig. 3). Some scars do occur below the lateral line but practically never on the head or posterior to the anal and adipose fins (i.e. on the caudal peduncle). The pattern of attack was similar for males and females (Fig. 3) and for the left and right sides of the body (Fig. 4).

Little information is available on the position of scars on other species of fish in Loch Lomond. Data for nine scarred trout caught in 1966 are given in Fig. 5, together with comparable data for nine scarred powan, taken at the same time as the trout. The plots suggest that the scars on trout are more dispersed on the sides of the body than in powan, but more material is needed to verify this.

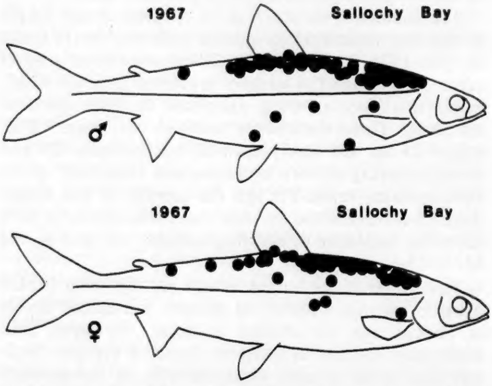

FIG. 3. The distribution of lamprey scars on male and female powan collected from Sallochy Bay in Loch Lomond in 1967.

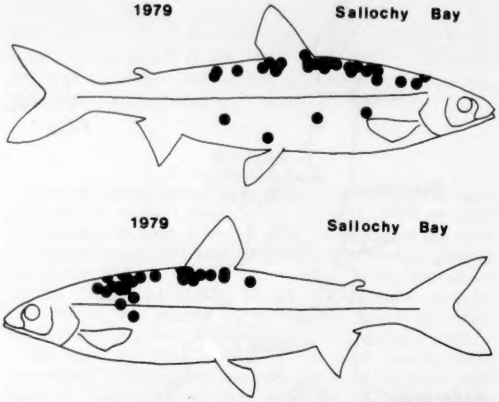

FIG. 4. The distribution of lamprey scars on the left and right sides of powan collected from Sallochy Bay in Loch Lomond in 1979.

EFFECT OF LAMPREY SCARS

The effect of attacks by lampreys on powan was examined by comparing the lengths and weights of unscarred and scarred fish. However, because lampreys attack larger fish (Fig. 2) the mean length of groups of unscarred powan is less than that of scarred powan (Table 3). Though the mean length of powan with only one scar is less than that of multiple scarred fish, there is virtually no difference in the mean lengths of fish with more than one scar.

A more realistic examination of the effect of scarring on length is obtained by comparing the mean lengths of unscarred and scarred fish of the same ages (Table 4). The surprising conclusion from the four age-groups

TABLE 3. The mean lengths of powan collected from Loch Lomond in 1966 in relation to the number of lamprey scars.

	Number of scars								
	0	1	2	3	4	5	6	7	8
No. of fish	273	79	48	30	23	7	2	3	2
Mean length (cm)	27.2	28.9	30.0	29.5	29.8	29.9	29.2	29.7	29.4

most abundant in the samples (5–8 yr old inclusive) is that, on average, scarred fish are larger than unscarred fish. In pairs of unscarred and scarred fish of exactly the same length, the weights plotted against one another showed that though, on average, the weight of scarred fish was less than that of unscarred fish, the difference is slight, and many scarred fish are heavier than unscarred fish of the same length.

SIZE OF SCARS

Well-defined healed scars on powan are usually oval in shape. Measurements of 20 scars on 15 powan showed that maximum lengths ranged from 10 to 18 mm and widths from 9 to 14 mm. As has been shown with the sea lamprey, it is likely that the sizes of these scars are related to the sizes of the oral discs of the river lampreys concerned (Lennon 1954).

Discussion

No data are available on lampreys attacking fish in freshwater in any other part of Great Britain, though occasional reports have been received of scarred fish (trout and pike) in Loughs Conn, Corrib, Leane, and Inniscanna in Ireland. Elsewhere in Europe, among the waters reported to contain populations of parasitic lampreys (*L. fluviatilis*), are lakes Onega and Ladoga, where lampreys attack cisco (*Coregonus albula*) and smelt (*Osmerus eperlanus*) (Berg 1962) as well as salmon (Abakumov 1960). Neither of these populations appears to have been studied. Tuunainen et al. (1980) report landlocked populations of river lampreys in several lakes in Finland. In North America, Heard (1966) records landlocked populations of the holarctic species of arctic lamprey, *Lethenteron japonicum* (Martens).

TABLE 4. The mean lengths of unscarred and scarred powan in relation to age. The sample was collected at Ross Point, Loch Lomond, in 1966.

	Unscarred fish		Scarred fish	
Age (yr)	Number	Mean length (cm)	Number	Mean length (cm)
3	1	22.3	0	—
4	6	26.1	1	28.0
5	15	27.3	8	28.1
6	19	27.9	17	28.3
7	5	28.0	15	28.4
8	4	28.2	5	29.0
9	3	29.6	1	27.9

In the Great Lakes of North America, however, populations of *P. marinus* took some time to become established, but once they reached the upper lakes, their range expanded rapidly and their numbers increased phenomenally (Smith 1971). Having established itself this species then contributed to the decimation of major fish stocks in Lakes Huron, Michigan, and Superior, and many commercial fisheries collapsed. Intensive research on lampreys in North America then followed and in contrast to Europe there is now enormous literature on their biology.

Though in any one lake one or a few host species appear to be favored for attack, a wide range of fish acts as hosts in North America. Thus Hubley (1961) records 17 different species being attacked by *Ichthyomyzon* in the Upper Mississippi River with northern pike (*Esox lucius*) as the favorite host. In Love Lake in Maine, landlocked *P. marinus* attacked 11 species, especially landlocked atlantic salmon (*Salmo salar*) but including also yellow perch (*Perca flavescens*) (Davis 1967). Neither pike nor perch are known to be attacked in Loch Lomond, but they are obviously potential hosts there.

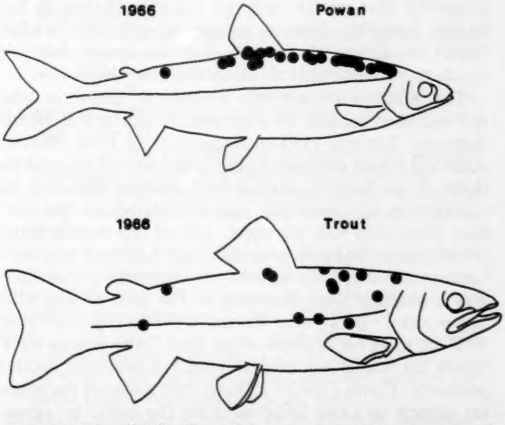

FIG. 5. The distribution of lamprey scars on powan and trout collected together in Loch Lomond in 1966.

The incidence of scarring of whitefish in Loch Lomond (26–50%) is clearly not unusual compared to other waters which have been studied. Thus though Hubley (1961) found a very low incidence (less than 1%) to be characteristic of fish in the Upper Mississippi River, Davis (1967) showed that 85% of salmon in Love Lake had been attacked. In Lake Huron, 35% of white suckers, *Catostomus commersoni*, had scars (Hall and Elliott 1954), while in Seneca Lake 90% of lake trout, *Salvelinus namaycush*, bore scars in 1927 (Gage 1928) and 88% in 1941. Pycha and King (1975) found that the percentage of lake trout scarred in Lake Superior was associated with the relative abundances of lamprey and trout.

Hall and Elliott (1954) with white suckers and Eschmeyer (1957) and Pycha and King (1975) with lake trout, and others have shown that as with powan in Loch Lomond there is a tendency for the medium to large fish to bear most scars. Eschmeyer (1957) believed that this was due to the fact that most small fish which were attacked, died. This is substantiated by the feeding experiments of Lennon (1954) where small fish attacked by lampreys in aquaria died much more often than larger ones. However, Farmer and Beamish (1973) have shown that large fish are attacked more frequently and Pycha and King (1975) suggest that the low percentage of small lake trout with lamprey wounds in Lake Superior was mainly a reflection of a low attack rate by sea lampreys rather than high mortality due to lamprey attacks.

Small powan (less than 25 cm) in Loch Lomond are apparently not subject to frequent attacks by lampreys, for even in large samples very few scarred or wounded specimens ever occur at any time of the year. Thus the low incidence of scars on small fish (Fig. 2) is more likely to be due to a real difference in attack rate by the parasite rather than a differential and heavier mortality rate in small attacked whitefish. It is suggested that powan undergo a major change in behavior (possibly from a pelagic to a partly benthic habit) at about 25 cm and that the larger fish are much more vulnerable to lampreys after this.

The position of lamprey wounds or scars on host fish has been studied by a number of workers in North America. Lennon (1954) found that in Lake Huron, scars were most common in the lower half of the middle third of the body in several host species. This was in contrast to his aquarium experiments where the surface most used was the upper half of the middle third of the host's body (i.e. as in Loch Lomond powan). Lennon explained this anomaly by suggesting that there was a much greater mortality in the lake of fish with upper scars. Berst and Wainio (1967) reported that 89% of scars on rainbow trout from Lake Huron were below the lateral line and between the head and caudal peduncle. Davis (1967) showed that 83% of the scars on salmon in Love Lake were on the belly. In agreement with most of these findings within North America, Farmer and Beamish (1973) found that 69% of the scars on various teleosts were below the lateral line between the head and tail. These data are in contrast to those from Loch Lomond where the distribution of scars would suggest that these are the main points of attachment, rather than the more likely ones to heal from attacks all over the body. The contrast between the consistent North American data and those from Loch Lomond (which is also very consistent) indicates that there are major differences in the behavioral relationships between host species and lampreys in the two situations. The fact that in North America *P. marinus* is the parasite, whereas in Scotland *L. fluviatilis* (apparently) is involved, may be most relevant.

In Loch Lomond it was observed that although the incidence of scarring increased with the size of the host powan, there was a tendency for a decrease in scarring in the few large fish examined. Pycha and King (1975) also observed that the few largest fish in catches tended to have no lamprey wounds, and that this occurred in several years. There is no obvious explanation for this phenomenon.

Multiple scarring appears to be a common feature of fish attacked by lampreys in various waters. Royce (1950) noted up to 10 scars or wounds in a single fish. Hubley (1961) and Davis (1967) record maxima of seven and eight scars, respectively, in the populations they studied. These are in accord with the maximum of nine scars found on a single powan in 1951 (see also Table 2).

Royce (1950) found that no demonstrable difference existed among the mean weights of the various groups of lake trout which had differing numbers of scars, and Slack (1955) found no loss of condition in powan scarred by lampreys. Similarly, Davis (1967) found that there was no indication that lampreys seriously affect salmon or other fish in Love Lake. The present data are in agreement with these findings and the conclusion is that, if they recover from attacks, the performance of host species is not affected seriously even when multiple wounds are involved.

In contrast, there is considerable evidence that lamprey attacks can cause major mortalities among some host populations. The collapse of some Great Lakes fisheries is the most outstanding example of this. Surface (1897) noted that many deaths resulted in fish attacked by lampreys in Cayuga Lake. Lennon (1954) found that in aquarium experiments up to 80% of fish attacked by lampreys died as a result. Spangler (1970) estimated that predation by sea lampreys on lake whitefish, *Coregonus clupeaformis*, was an important component in their mortality.

In Loch Lomond, dying or dead powan are occasionally found with lamprey wounds and even lampreys attached to them. Such mortalities have been noted by Gray (1864), Robertson (1875), Lumsden and Brown (1895), Lamond (1922), and the present author. Though dead or dying fish are rarely common in Loch Lomond — except at times of epidemics (Roberts et al.

1970) — those which have been found during this study have invariably carried several lamprey wounds.

Loch Lomond is unique in several aspects. It is already outstanding in being the largest area of water in Great Britain with an unusual dual character. It contains more fish species than any other loch in Scotland, and is one of only two lochs in Scotland where whitefish (*C. lavaretus*) occur. Parasitism of this fish by lampreys seems to be a unique situation in freshwater in Great Britain and occurs in only a few other places in Europe. In none of these places has the ecology of the lampreys been studied in detail (Tuunainan et al. 1980).

The study of the lamprey population in Loch Lomond is therefore of considerable interest and relevant to the major problems being experienced in North America. It is important that further research is carried out, aimed specifically at answering problems concerning lampreys in Loch Lomond. The adults in particular merit special attention. It is not known for instance whether the lampreys feeding there are landlocked or anadromous, or what the relationship between *L. fluviatilis* and *P. marinus* may be. The effect of lamprey parasitism on the mortality and performance of host fish populations, especially whitefish, is of considerable importance. Finally, the major question remains to be answered: why is Loch Lomond apparently unique among British lakes in possessing a large population of lampreys feeding in freshwater?

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ABAKUMOV, V. A. 1960. The damage done by lampreys to fish stocks. Rybn. Khoz. 35: 32–33.

BERG, L. S. 1962. Freshwater fishes of the U.S.S.R. and adjacent countries. (Transl. from Russian by the Israel Program for Scientific Translations, Jerusalem.)

BERST, A. H., AND A. A. WAINIO. 1967. Lamprey parasitism of rainbow trout in southern Georgian Bay. J. Fish. Res. Board Can. 24: 2539–2548.

BROWN, A. 1891. The fishes of Loch Lomond and its tributaries. Scot. Nat. 10: 114–124.

DAVIS, R. M. 1967. Parasitism by newly-transformed anadromous, sea lampreys on landlocked salmon and other fishes in a coastal Maine Lake. Trans. Am. Fish. Soc. 96: 11–16.

ESCHMEYER, P. M. 1957. The near extinction of lake trout in Lake Michigan, Trans. Am. Fish. Soc. 85: 102–119.

FARMER, G. F., AND F. W. H. BEAMISH. 1973. Sea lamprey (*Petromyzon marinus*) predation on freshwater teleosts. J. Fish. Res. Board Can. 30: 601–605.

GAGE, S. H. 1928. The lampreys of New York State — life history and economics. Rep. N.Y. State Conserv. Dep. 17: 158–191.

GRAY, R. 1864. Quadrupeds, birds and fishes of Loch Lomond and its vicinity. Keddie, Glasgow, Scotland.

HALL, A. E., AND O. R. ELLIOTT. 1954. Relationship of length of fish to incidence of sea lamprey scars on white suckers, *Catostomus commersoni*, in Lake Huron. Copeia 1: 73–74.

HEARD, W. R. 1966. Observations on lampreys in the Naknek River system of southwest Alaska. Copeia 2: 332–339.

HUBLEY, R. C. 1961. Incidence of scarring on fish in the upper Mississippi River. Trans. Am. Fish. Soc. 90: 83–85.

HUNTER, W. R., H. D. SLACK, AND M. R. HUNTER. 1959. The lower vertebrates of the Loch Lomond district. Glasg. Nat. 18: 84–90.

LAMOND, H. 1922. Some notes on two of the fishes of Loch Lomond: the powan and the lamprey. Fish. Scotl. Salmon Fish. 1923: 3–10.

1931. Loch Lomond. Jackson, Glasgow, Scotland.

LENNON, R. E. 1954. Feeding mechanism of the sea lamprey and its effect on host fishes. Fish. Bull. Fish. Wildl. Serv. 56: 247–293.

LUMSDEN, J., AND A. BROWN. 1895. A guide to the natural history of Loch Lomond and neighbourhood. Bryce, Glasgow, Scotland.

MACDONALD, T. H. 1959. Estimates of length of larval life in three species of lamprey found in Britain. J. Anim. Ecol. 28: 293–298.

MAITLAND, P. S. 1966a. Present status of known populations of the vendace, *Coregonus vandesius* Richardson, in Great Britain. Nature, Lond. 210: 216–217.

1966b. The fauna of the River Endrick. Glasg. Univ. Publ. Stud. Loch Lomond 2: 1–194.

1967a. Echo sounding observations on the Lochmaben vendace, *Coregonus vandesius* Richardson. Trans. Dumfr. Gall. Nat. Hist. Soc. 44: 29–46.

1967b. The artificial fertilisation and rearing of the eggs of *Coregonus clupeoides* Lacépède. Proc. R. Soc. Edin. B, 70: 82–106.

1969. The reproduction and fecundity of the powan, *Coregonus clupeoides* Lacépède, in Loch Lomond, Scotland. Proc. R. Soc. Edin. B, 70: 233–264.

1970. The origin and present distribution of *Coregonus* in the British Isles. Proc. Int. Symp. Biol. Coregonid Fish. 1: 99–114.

1972. Loch Lomond: Man's effects on the salmonid community. J. Fish. Res. Board Can. 29: 849–860.

MILLS, D. H. 1969. The growth and population of roach in some Scottish waters. Proc. Br. Coarse Fish. Conf. 4: 50–57.

PARNELL, R. 1838. Observations on the *Coregoni* of Loch Lomond. Ann. Mag. Nat. Hist. 1: 161–165.

POTTER, I. C., AND T. S. OSBORNE. 1975. The systematics of British larval lampreys. J. Zool. 176: 311–329.

PYCHA, R. L., AND G. R. KING. 1975. Changes in the lake trout population of southern Lake Superior in relation to the fishery, the sea lamprey, and stocking, 1950–70. Gt Lakes Fish. Comm. Tech. Rep. 28: 1–34.

ROBERTS, R. J., J. LECKIE, AND H. D. SLACK. 1970. 'Bald spot' disease in powan *Coregonus lavaretus* (L.) J. Fish Biol. 2: 103–106.

ROBERTSON, D. 1875. On *Petromyzon fluviatilis* and its mode of preying on *Coregonus clupeoides*. Proc. Nat. Hist. Soc. Glasg. 2: 61–62.

ROYCE, W. F. 1950. The effect of lamprey attacks upon lake trout in Seneca Lake, New York. Trans. Am. Fish. Soc. 79: 71–76.

SHAFI, M., AND P. S. MAITLAND. 1971a. The age and growth of perch, *Perca fluviatilis* L. in two Scottish lochs. J. Fish. Biol. 3: 39–57.

1971b. Comparative aspects of the biology of pike, *Esox lucius* L., in two Scottish lochs. Proc. R. Soc. Edin. B, 71: 41–60.

SLACK, H. D. 1955. Factors affecting the productivity of *Coregonus clupeoides* Lacépède in Loch Lomond. Ver. Int. Verh. Limnol. 12: 183–186.

1957. Physical and chemical data. Glasg. Univ. Publ. Stud. Loch Lomond. 1: 14–26.

SLACK, H. D., F. W. K. GERVERS, AND J. D. HAMILTON. 1957. The biology of the powan. Glasg. Univ. Publ. Stud. Loch Lomond 1: 113–127.

SMITH, B. R. 1971. Sea lampreys in the Great Lakes of North America. *In* M. W. Hardisty, and I. C. Potter [ed.] The biology of lampreys. Academic Press, London.

SPANGLER, G. R. 1970. Factors of mortality in an exploited population of whitefish, *Coregonus clupeaformis*, in northern Lake Huron, p. 515–529. *In* C. C. Lindsey and C. S. Woods [ed.] Biology of coregonid fishes. University of Manitoba Press, Winnipeg, Man.

STUART, J. 1796. Parish of Luss. Stat. Acc. Scot. 1: 238–271.

SURFACE, H. A. 1897. The lampreys of central New York. Bull. U.S. Fish. Comm. 17: 209–215.

TUUNAINEN, P., E. IKONEN, AND H. AUVINEN. 1980. Lampreys and lamprey fisheries in Finland. Can. J. Fish. Aquat. Sci. 37: 1953–1959.

Classification of Sea Lamprey (*Petromyzon marinus*) Attack Marks on Great Lakes Lake Trout (*Salvelinus namaycush*)[1,2]

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KING, E. L. JR. 1980. Classification of sea lamprey (*Petromyzon marinus*) attack marks on Great Lakes lake trout (*Salvelinus namaycush*). Can. J. Fish. Aquat. Sci. 37: 1989–2006.

Criteria for the classification of marks inflicted by sea lamprey (*Petromyzon marinus*) into nine categories were developed from laboratory studies in an attempt to refine the classification system used in field assessment work. These criteria were based on characteristics of the attachment site that could be identified under field conditions by unaided visual means and by touching the attachment site. Healing of these marks was somewhat variable and was influenced by the size of lamprey, duration of attachment, severity of the wound at lamprey detachment, season and water temperature, and by other less obvious factors. Even under laboratory conditions staging of some wounds was difficult, especially at low water temperatures. If these criteria are to be used effectively and with precision in the field, close examination of individual fish may be required. If the feeding and density of specific year-classes of sea lampreys are to be accurately assessed on an annual basis, close attention to the wound size (as it reflects the size of the lamprey's oral disc) and character of wounds on fish will be required as well as consideration of the season of the year in which they are observed.

Key words: sea lamprey, attack marks, lake trout, Great Lakes

KING, E. L. JR. 1980. Classification of sea lamprey (*Petromyzon marinus*) attack marks on Great Lakes lake trout (*Salvelinus namaycush*). Can. J. Fish. Aquat. Sci. 37: 1989–2006.

Des études en laboratoire ont permis d'établir des critères de classification des marques infligées par la grande lamproie marine (*Petromyzon marinus*) en neuf catégories, dans le but d'améliorer le système de classification utilisé dans les évaluations sur le terrain. Ces critères sont fondés sur les caractéristiques du site de fixation indentifiables sur le terrain à l'oeil nu et par toucher. La cicatrisation de ces marques est quelque peu variable et est affectée par la taille de la lamproie, durée de fixation, sévérité de la blessure au moment du détachement de la lamproie, saison et température de l'eau, et autres facteurs moins évidents. Même dans des conditions de laboratoire, certaines blessures sont difficiles à classer, surtout aux basses températures de l'eau. Si ces critères doivent être utilisés efficacement et avec précision sur le terrain, il faudra peut-être examiner le poisson un à un avec soin. Pour évaluer avec précision l'alimentation et la densité de classes d'âge spécifiques de lamproie marine sur base annuelle, on devra porter une attention particulière à la taille de la blessure (elle reflète la grosseur du disque oral de la lamproie) et au caractère des blessures sur les poissons, ainsi que la saison à laquelle sont faites les observations.

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BIOLOGICAL and economical consequences of the spread of the sea lamprey (*Petromyzon marinus*) in the upper Great Lakes have been documented by several investigators (Hile et al. 1951a; Loftus 1958; Eschmeyer 1957; Fry and Budd 1958; Lawrie 1970). The sea lamprey's destructive impact on the valuable sport and commercial fisheries of these lakes was sufficient to justify a program to study its natural history and develop methods to control its abundance. A research and control program has been sponsored by the Great Lakes Fishery Commission since 1955. The sea lamprey population in Lake Superior has been reduced by about 90% from precontrol levels by the use of selective lampricides (Smith et al. 1974). Equivalent quantitative data on the reduction of sea lamprey populations in the other Great Lakes are not available, but the control efforts in those lakes are believed to have produced nearly the same results.

The major biological issue is whether the present level of sea lamprey control will allow for the reestablishment of naturally sustained fish stocks — especially

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[1] This paper forms part of the Proceedings of the Sea Lamprey International Symposium (SLIS) convened at Northern Michigan University, Marquette, Michigan, July 30–August 8, 1979.

[2] Contribution No. 553 from the Great Lakes Fisheries Laboratory, Ann Arbor, Michigan.

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lake trout (*Salvelinus namaycush*), not only in Lake Superior, but also in the other Great Lakes. The present level of control appears to be adequate with intensive hatchery propagation of lake trout and other species. Additional knowledge was needed on the impact of residual sea lampreys on Great Lakes fish stocks to meet better the management objectives of the entire program. Attempts have been made to measure the impact of sea lampreys on Great Lakes fish stocks by determining the incidence of lamprey-inflicted wounds and scars on surviving fish. For research and management agencies to use sea lamprey-inflicted marks as indicators of lamprey abundance and their parasitic activity, it is necessary that reports from the field be as consistent as possible. Consistency among observers reporting on the incidence and post-attack character of sea lamprey-inflicted marks on Great Lakes fish has been lacking because no uniform criteria for classifying these marks have existed. Most of the terminology and criteria used in reporting on these marks were developed from field observations (Fry and Budd 1958; Pycha and King 1975). The lack of consistency in reporting on the character of sea lamprey attack marks on fish has made field data difficult to interpret. The confidence in the reliability of data collected from the field can be improved by uniform and consistent reporting on the incidences, character, and recentness of sea lamprey-inflicted marks on fish.

Research was needed, therefore, to develop standard criteria for improving the accuracy in classifying sea lamprey-inflicted marks on fish and for determining with greater precision when they were made. The present study was conducted in response to requests from representatives of various Great Lakes fishery agencies for data that would provide these criteria for use in classifying sea lamprey attack marks observed on lake trout under field conditions. The major objective of the present study was to develop standard criteria for classifying sea lamprey-inflicted marks to permit (1) more refined indices of the intensity of sea lamprey predation on lake trout stocks throughout the Great Lakes, and (2) more precise estimates of sea lamprey-induced mortality in those stocks.

Materials and Methods

Laboratory studies were conducted to describe the sequential stages of healing of sea lamprey-inflicted marks on lake trout. Lake trout were selected as the test fish because many of the questions regarding sea lamprey/host interactions involve the lake trout, a species very important in the Great Lakes from both ecological and economical considerations. Lake trout and sea lamprey were placed in "Living Stream" tanks (0.52 m wide, 0.55 m deep, and 2.07 m long) supplied with Lake Huron water. The fish and lamprey were weighed and measured before being released. The tanks held 578 L of water into which Lake Huron water was added at the rate of 3.6 L/min. Water temperatures were controlled by the use of special heating or refrigeration equipment. Heated or chilled water was either pumped or siphoned from constant temperature troughs into test tanks, or immersion equipment (either heating or refrigeration) was installed directly into the tanks. Usually one lamprey and one trout were placed into each tank. Occasionally, as many as two lake trout and four lampreys were held in each tank until a single lamprey attached to a trout, at which time the rest of the specimens were moved to other tanks. For identification purposes, the lake trout were fin-clipped (right or left pectoral) and the lampreys individually marked by injection of fluorescent dye into the dorsal fin using the method developed by Hanson (1972).

Lampreys were allowed to remain attached to the trout until they detached of their own accord. Within 8–16 h after detachment, the fish and lamprey were reweighed and measured, the wound site described and photographed, and the fish placed in a recovery tank. As many as four fish with wounds or scars were held in separate recovery tanks at regulated water temperatures. The individual fish were assigned a number and the lamprey wound it bore served as a distinctive identifying mark for that fish for as long as it was under observation. MS-222 was used as an anesthetic, at a concentration of 50 mg/L in Lake Huron water, when handling of the fish or lamprey was required.

Periodically, after the lamprey detached, the wound sites on the trout were described and photographed to document healing. Individual data sheets were kept for each wounded fish. At each observation time the fish was anesthetized, notes made on the healing progress of the wound, and photographs taken of the wound site. Photographs were taken more frequently during the early stages of healing and less frequently as the wounds reached the latter stages of healing when tissue regeneration slowed. Photographs were taken with a Honeywell Pentax 35-mm camera, equipped with a Macro-Takumar lens designed to give maximum balance of optical contrast and resolution at close range. Most photographs were taken at 110 mm from the outer ring of the lens (fully extended) to the subject. Some, however, were taken at further distances, according to the size of the wound to be included in the field of view. Wounded or scarred fish were anesthetized and placed in a 40-L glass aquarium containing Lake Huron water, tempered the same as that from which the fish came. The area to be photographed was positioned against the inside of the aquarium glass, under a superimposed metric rule and identifying serial number. Photographs were taken through the aquarium glass. The aquarium in which the wounded fish were photographed was illuminated by 10 Magnalux Luxor 40-W fluorescent lamps hung from the ceiling in a corner of a laboratory room (area 4 m^2), which provided adequate light for the type of film and camera used.

Lake trout used in these experiments came from three sources. Surplus brood stock were provided by the Marquette State Fish Hatchery, Marquette, Michigan. Smaller lake trout, reared at the Great Lakes Fishery Laboratory, Ann Arbor, Michigan, and at the Jordan River National Fish Hatchery, Elmira, Michigan, were also used. Two feeding classes of sea lamprey were used in the experiment. One group was obtained as downstream migrants (recently metamorphosed) from the Big Garlic River, Marquette County, Michigan. Another group was purchased as parasitic adults from a commercial fisherman trap-netting in Hammond Bay of Lake Huron.

Each test tank having lamprey and fish together was checked at least twice daily to determine attachments or detachments by lampreys. Each recovery tank, containing

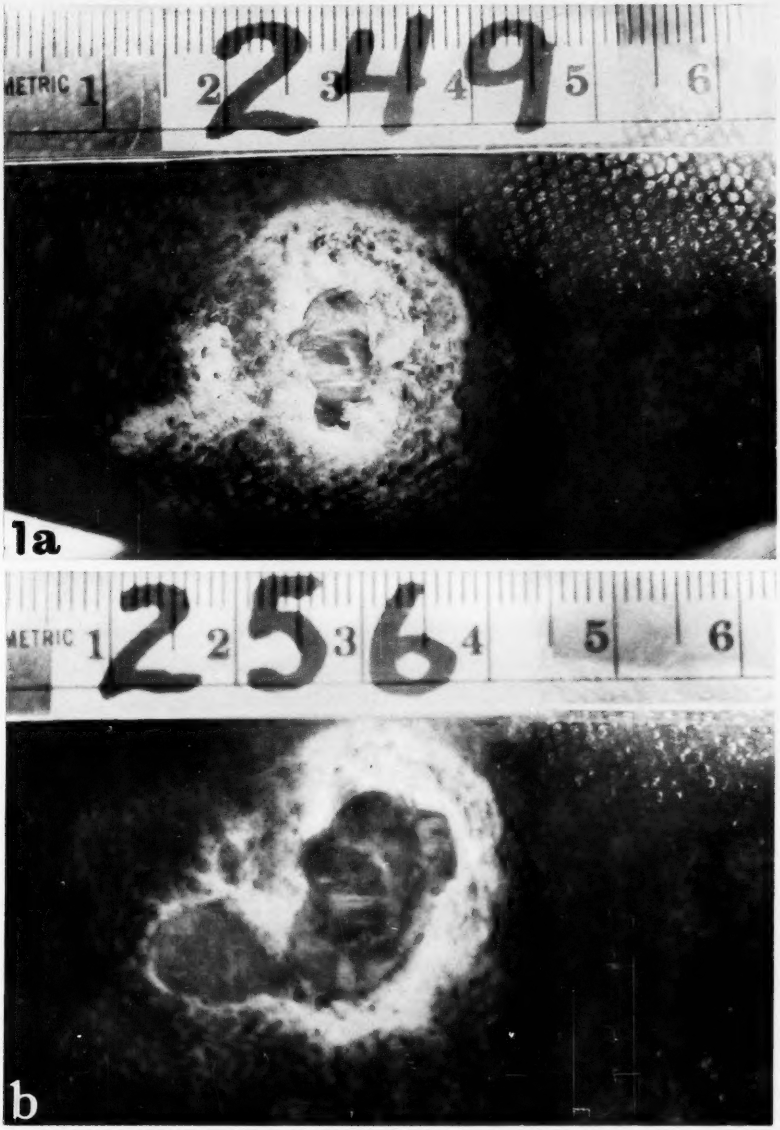
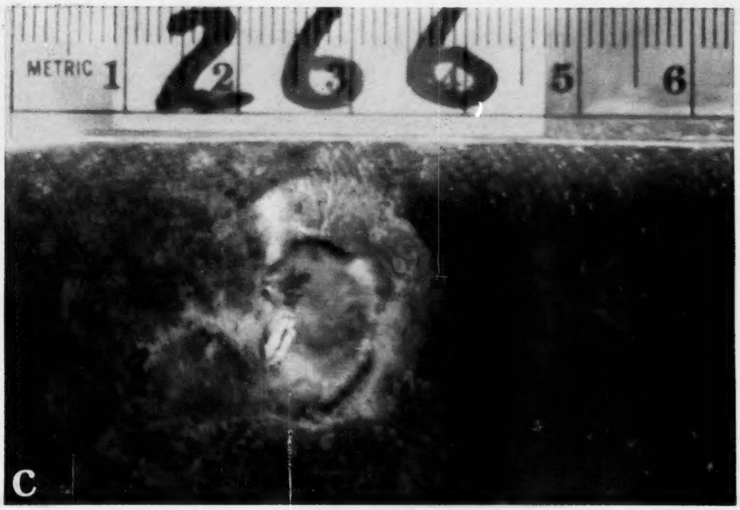


FIG. 1a. 10.0°C, day 1. Attack mark on 485-mm lake trout produced by lamprey 4.5 g, with oral disc 14 mm before attachment, and 50.0 g and oral disc 28 mm at detachment at 82 d. *Location:* Middle of back between head and dorsal fin. *Classification:* Type A, Stage I. *Description:* Skin broken exposing musculature; attachment site rough to the touch and descaled; 3-mm-deep pit can be seen and felt in musculature; pit surrounded by ragged, white, necrotic tissue; hemorrhaged tissue present at margins of site.

FIG. 1b. Day 9. *Classification:* Type A, Stage II. *Description:* Entire attachment site smooth to the touch, pit partly filled with semiopaque, mucous-like material; pit can be seen and felt as an indentation; necrotic tissue has sloughed exposing more musculature; site no longer ragged in appearance.



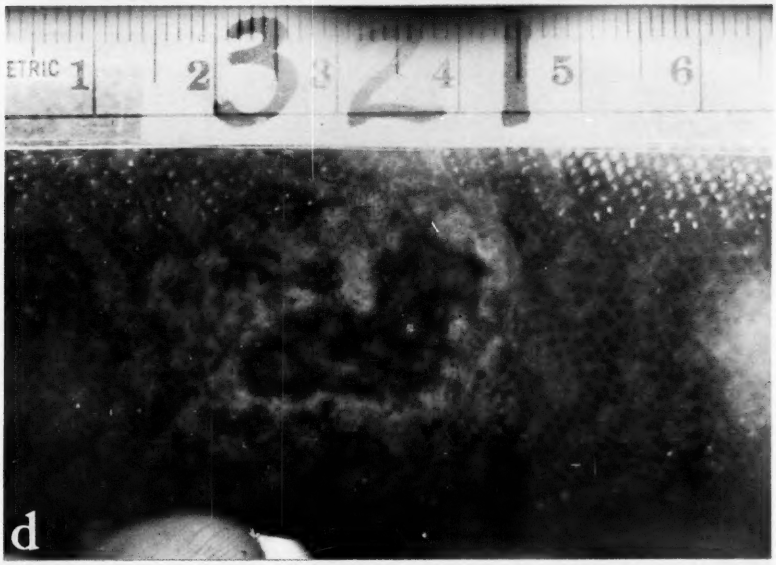
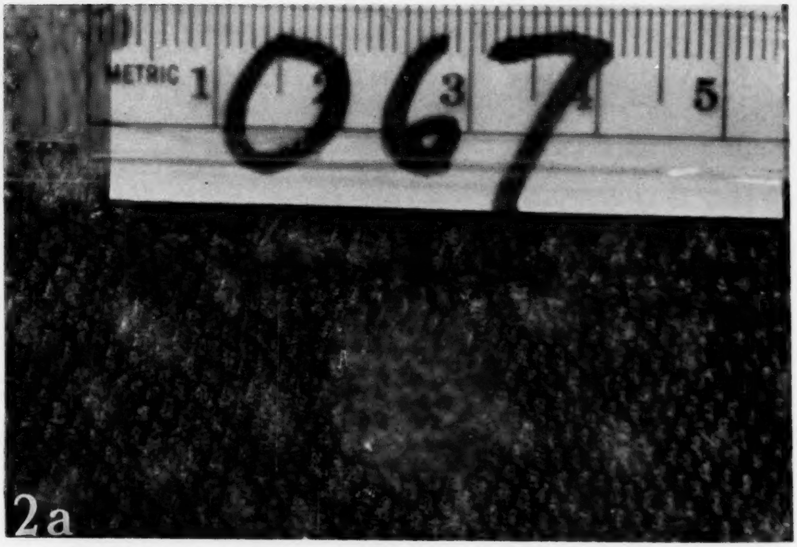


FIG. 1c. Day 30. *Classification:* Type A, Stage III. *Description:* Repigmentation of site underway; new dark pigment most visible at edge of exposed musculature and covering previously exposed musculature in lower left portion of site; pit filling with new tissue, but can still be felt as an indentation.

FIG. 1d. Day 133. *Classification:* Type A, Stage IV. *Description:* Repigmentation complete; an indentation can still be felt at site; scale regeneration not evident.



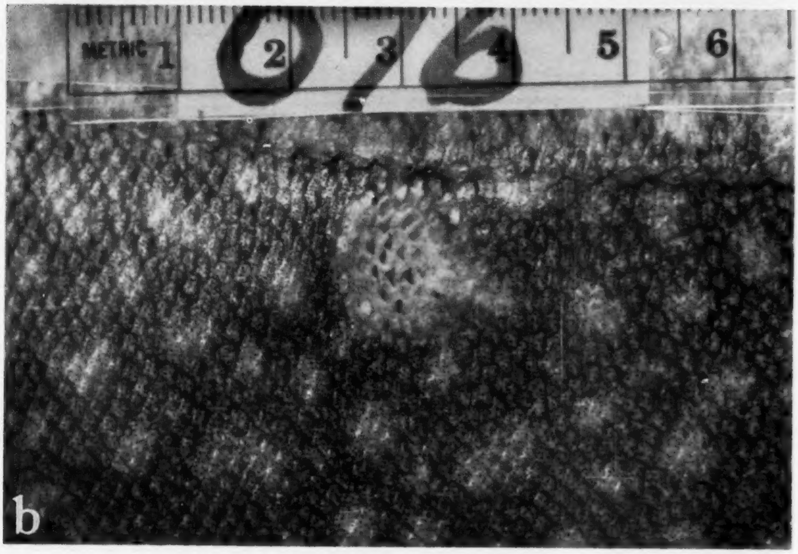
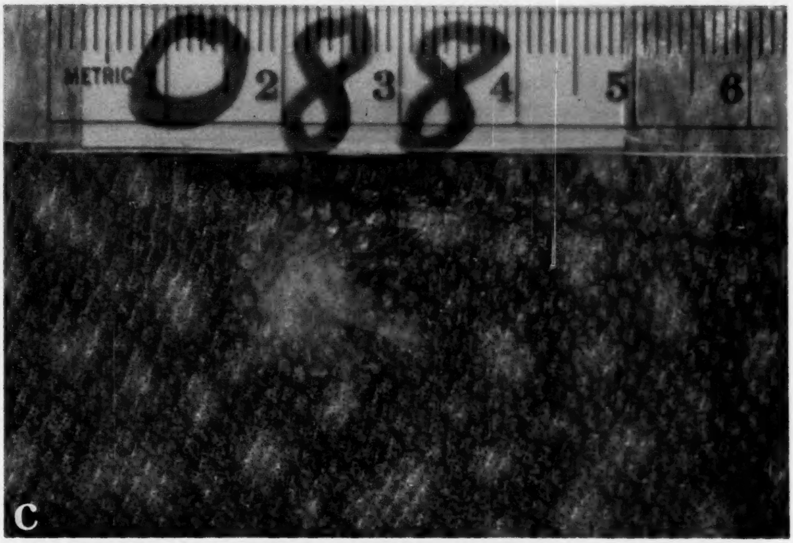


FIG. 2a. 10.0°C, day 0. Attack mark on 623-mm lake trout produced by 7.0-g lamprey with oral disc 15.0 mm before attachment and 9.0 g and oral disc 16.0 mm at detachment at 10 d. *Location:* Immediately below lateral line about 50 mm behind head. *Classification:* Type B, Stage I. *Description:* No break in skin exposing musculature; attachment site rough to the touch, descaled, and hemorrhaged.

FIG. 2b. Day 15. *Classification:* Type B, Stage II. *Description:* Smooth to the touch.

[illegible]



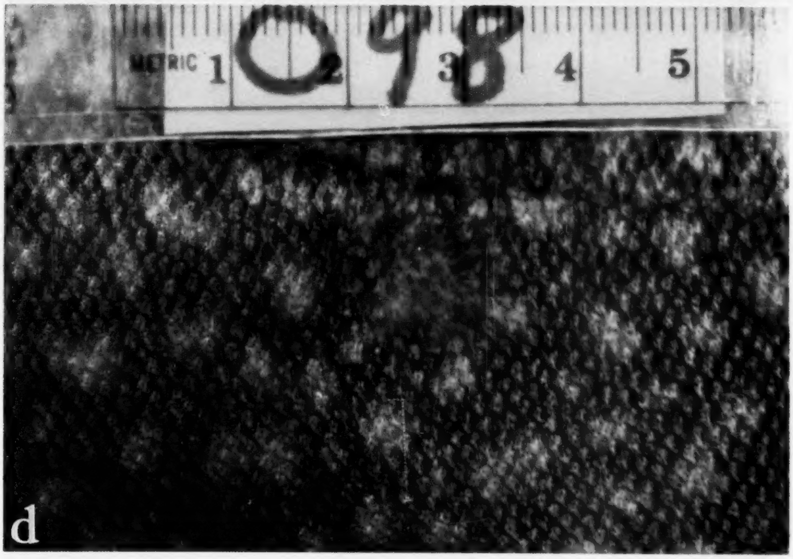
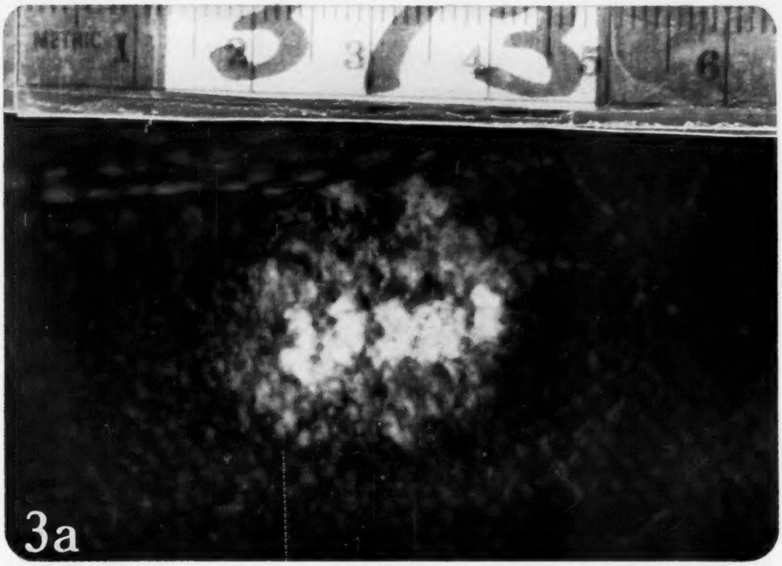


FIG. 2c. Day 29. *Classification:* Type B, Stage III. *Description:* No hemorrhaged tissue visible; new, dark pigment visible in margins of descaled area.

FIG. 2d. Day 50. *Classification:* Type B, Stage IV. *Description:* Repigmentation appears complete; irregularly arranged, regenerated scales forming at margins of descaled area.

[illegible]



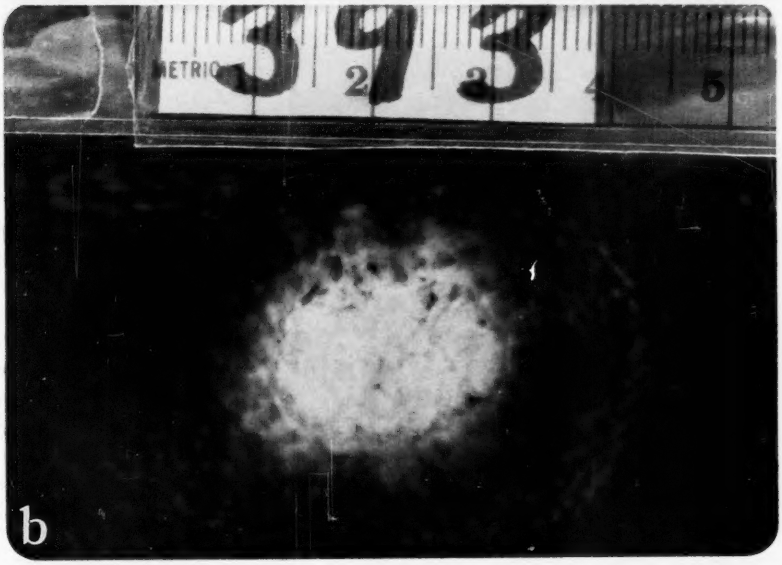


FIG. 3a. 4.0°C, day 0. Attack mark on 642-mm lake trout produced by 200.0-g lamprey with oral disc of 38.0 mm. Lamprey was attached for 2 d and did not grow. *Location:* Base of dorsal fin. *Classification:* Type B, Stage I. *Description:* No break in skin exposing musculature; attachment site rough to the touch, pit can be felt in musculature beneath skin.
FIG. 3b. Day 14. *Classification:* Type B, Stage I. *Description:* Covered with whitish-yellow necrotic tissue.

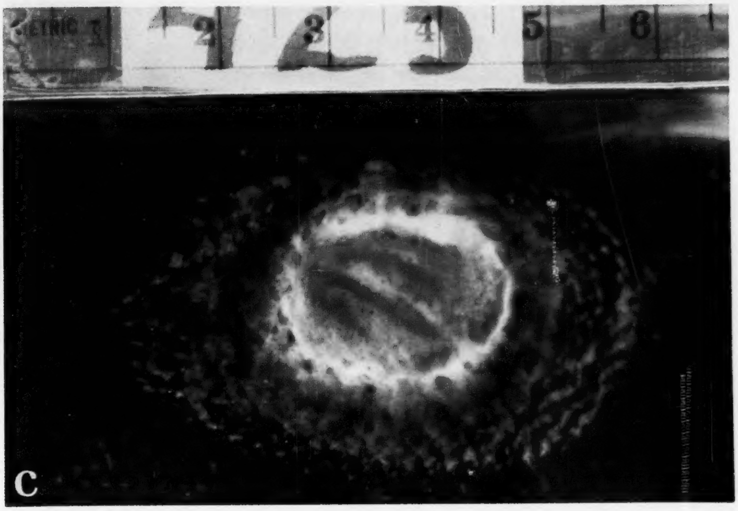
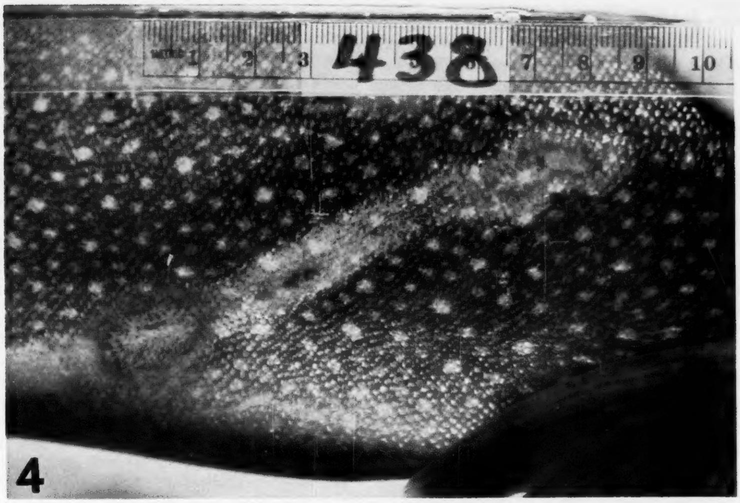


FIG. 3C. Day 32. *Classification:* Type A, Stage I. *Description:* Whitish-yellow necrotic tissue has sloughed exposing musculature; entire site still not smooth to touch.

[illegible]



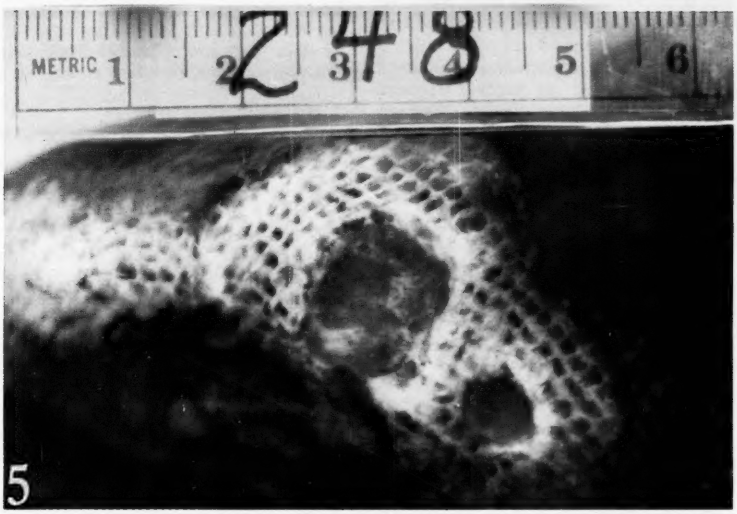


FIG. 4. 10.0–4.0°C, day 68. Attack mark on 610-mm lake trout produced by 7.4-g lamprey with oral disc 15.0 mm before attachment and 11.0 g and oral disc 16.0 mm at detachment at 30 d. *Location:* Midbody, right side. *Classification:* Type B, Stage I. (Based on major attachment site in earliest stage of healing.) *Description:* Elongated attack mark with multiple attachment sites; major attachment site in lower left portion of figure has typical Type B, Stage I characteristics.

FIG. 5. 10.0°C, day 7. Attack mark on 627-mm lake trout produced by 22.9-g lamprey with oral disc 15.0 mm before attachment and 80.0 g and oral disc 30.0 mm at detachment at 43 d. *Location:* Dorsal surface left of midline behind head. *Classification:* Type A, Stage I. (Based on major attachment site in earliest stage of healing.) *Description:* Multiple major attachment sites. Site in lower right portion of figure has typical Type A, Stage II characteristics; sites in central and upper left have typical Type A, Stage I characteristics.

[illegible]

wounded or scarred fish, was checked daily to determine the condition of the fish. The wounded or scarred tissue of any trout that died, or from fish that were sacrificed because of poor condition, was excised and preserved in buffered formalin; these tissues will be subjected to histological studies in the future to define better the healing process of sea lamprey-inflicted marks on salmonids. The trout were offered Oregon Moist pellets on alternate days, and excess food, waste products, sediments, etc. were removed from the tanks the day after feeding.

Wound healing studies were conducted at four temperature regimes: 10.0°C; 10.0–4.0°C; 4.0°C; and 0.0–1.0°C. Trout wounded during the summer were held at 10.0°C; trout bearing fresh wounds in early fall were acclimated to falling water temperatures (10.0–4.0°C) and allowed to heal at a test temperature of 4.0°C over winter until spring, at which time survivors were acclimated back up to 10.0°C in synchrony with the rising lake water temperature. Another group, wounded at 4.0°C, was allowed to heal at 4.0°C, while a final group was held at ambient lake water temperatures over winter (0.0–1.0°C) to provide information on wounding and wound healing at this low temperature. The survivors from the 4.0°C and 0.0–1.0°C were also acclimated to 10.0°C with the rising lake temperature in the spring.

Over 300 lake trout were used in this study from which 46 complete case histories were obtained on individual fish which carried single attack marks. It was from these 46 case histories that the criteria for attack mark classification was developed.

Results and Discussion

The mechanism by which sea lampreys attach to hosts and create a mark or wound on teleost fish has been described by Gage (1929), Lennon (1954), and others. Farmer et al. (1975), in a laboratory study designed to determine the food consumption of sea lamprey, considered feeding to have occurred when a wound was produced on a host fish, but did not type or classify these wounds. The effort in the present study was to describe as accurately as possible each lamprey-inflicted mark, produce a photographic case history as the marks healed following detachment, and identify regenerating tissues and other distinguishing features as they appeared during the healing process. From these laboratory observations it was possible to develop criteria for typing and staging attack marks based on characteristics that could be discerned under field conditions by viewing and touching the attack mark and the adjacent body surface of the trout. These criteria were also based on observations from live or freshly killed lake trout that exhibited coloration typical of the live state. They should also be valid for classifying marks on lake trout that have undergone postmortem color change, although closer examination of the fish and the attack mark would probably be necessary for classifying the attack mark under field conditions.

ATTACK MARK CLASSIFICATION

Two basic types of sea lamprey attack marks were observed on lake trout, each with four stages of healing that were identifiable by unaided visual means and by touching the mark site.

The classification criteria for the two types of attack marks and their stages of healing are as follows.

Type A — The skin at the attachment site is broken exposing the underlying musculature. Damage is variable. *Stage I* — The lamprey has very recently detached. The underlying musculature is exposed. The site is rough to the touch and (if on a portion of the fish normally covered with scales) has been descaled. A pit can be seen and felt in the exposed musculature and the surrounding skin is white, necrotic, ragged in appearance, and hemorrhaged, but probably not bleeding (Fig. 1a). Bleeding from fresh, lamprey-inflicted attack marks on lake trout has been reported by some observers in the field. Bleeding was never observed from an attack mark on any of the lake trout in the present study, perhaps because the attack marks were not observed soon enough after the lamprey detached.
Stage II — The entire attachment site is covered with a transparent, membrane-like material and is smooth to the touch (this smooth membrane is the key character for this stage); the exposed musculature is usually pink in color. A pit can be seen and felt in the exposed musculature; a semiopaque, mucous-like material can be seen partly filling the pit. Unsloughed, white, necrotic skin and hemorrhaged tissue is usually visible (Fig. 1b).
Stage III — The attachment site is generally similar to that described for Stage II, but masses of new, dark, pigment cells partly cover the exposed musculature (visible pigmentation within the damaged area is the key character for this stage). These pigment cell masses are usually first visible at the edge of the descaled skin surrounding the exposed musculature; a pit can be felt and sometimes seen at the site (Fig. 1c).
Stage IV — The attachment site is similar in appearance to the adjacent, unaffected body surface of the trout; repigmentation is essentially complete. Scale regeneration (if the site would normally be covered with scales) has not begun; a slight pit or indentation can be felt at the site (Fig. 1d).

Type B — The attachment site appeared as an abrasion or an elongated scrape with no visible break through the integument. *Stage I* — The lamprey has very recently detached. The attachment site is rough to the touch and (if on a portion of the fish normally covered by scales) is descaled; the skin is basically intact and hemorrhaged, but probably not bleeding. The underlying musculature is not exposed; the site is firm to the touch, little or no swelling can be seen, and a pit cannot be felt in the underlying musculature (Fig. 2a). This attack mark heals to produce a Type B, Stage II mark.
Stage II — The attachment site is generally similar in appearance as in Stage I, except that a transparent, membrane-like material covers the entire site rendering it smooth to the touch; hemorrhaged skin tissue is

usually confined to the central portion of the site (Fig. 2b).

Stage III — The attachment site is smooth to the touch and appears as a lightly pigmented, or slightly blanched area; hemorrhaged tissue is not visible. Scale regeneration (if the site is one that would normally be covered by scales) has not begun (Fig. 2c).

Stage IV — The attachment site is closely similar in appearance to the adjacent, unaffected body surface; repigmentation is complete. If the site is one that would normally be covered with scales, it will be partly or fully covered with irregularly arranged, regenerated scales that may reflect light differently than the body surface immediately surrounding the site (Fig. 2d).

If the attachment site is swollen and a pit can be felt beneath the skin in the musculature, the skin has the potential to slough away (Fig. 3a and b) exposing the underlying tissue and developing into a Type A, Stage I mark (Fig. 3c). I classified this as a "sloughing" Type B, Stage I attack mark, distinguished by the spongy texture, presence of a pit beneath, and a slight swelling of the site.

Although some sea lampreys remain in one place while they are attached to the trout and produce attack marks that are relatively simple to classify (Fig. 1–3), other lampreys change their location (Fig. 4 and 5) sometimes producing both Type A and Type B marks and marks in different stages of healing on the same trout. These complex marks can be classified on the basis of the characteristics of the portion of the attachment site that is in the earliest stage of healing. For example, when both Stage I and Stage II marks of the same type are present on a fish, the earlier (Stage I) classification should be assigned to the attack mark as a whole; similarly, if one portion of the attachment site displays Type A, Stage II, and another portion shows Type B, Stage I characteristics, the Type B, Stage I designation should be applied to the entire mark.

Finally, if attack marks observed on lake trout during the early winter–late spring are to be classified so as to permit them to be attributed to a particular feeding year-class of sea lampreys, the size of the mark (as it reflects the diameter of the lamprey's oral disc and the size of the lamprey) should also be recorded. Generally, "small" attack marks observed in early winter–late spring can be attributed to the feeding year-class of lampreys with oral disc diameters of 20 mm or less entering the lakes at that time; "large" attack marks observed at that time are produced by the feeding year-class of lampreys with oral disc diameters of 30 mm or more that entered the lakes 1 year earlier.

The Type A and B marks I observed were undoubtedly the "complete" and "incomplete" wounds described by Lennon (1954). He classified a wound as complete if the skin of the prey fish was pierced. The wounds were classed as incomplete if the skin was not punctured but scales displaced with minimal damage to the skin surface. Mortality occurred among fish attacked by sea lamprey in the present study, but since I was unable to provide individual control fish for each fish attacked by lampreys, I was unable to correlate lamprey attachments with fish mortality. The Type A wound observed in this study was usually caused by an attachment of long duration by small lampreys which grew as they fed, or by large, actively feeding individuals. The Type B wound was usually caused by attachments of short duration by sea lampreys, large or small.

According to Van Oosten (1957), superficial injuries of the epithelium are readily repaired by the cells from the margin of the wound. The wound is closed by the secretion of a mass of mucus which is mixed with lymphocytes. A thin protective layer is formed by proliferating cells advancing from the wound margin into the damaged area. It is assumed that this process occurred during the latter phase of Stage I and into Stage II of our Type B marks. The healing of deep injuries, described by Van Oosten (1957), was probably very similar to the process of healing in our Type A marks. He describes these deep injuries as filling rapidly with a fairly clear transudate and a film-forming fibrin mixed with red corpuscles and other tissue. These tissues probably constituted the semiopaque, mucous-like material which appeared in the Type A, Stage II marks observed in the present study. In the latter stages of healing observed in the present study the subcutaneous area probably filled with granulated tissue formed from the connective tissue.

ESCHMEYER, P. H. 1957. The near extinction of lake trout in Lake Michigan. Am. Fish. Soc. 85: 102–119.

FARMER, G. J., F. W. H. BEAMISH, AND G. A. ROBINSON. 1975. Food consumption of the adult landlocked sea lamprey, *Petromyzon marinus* L. Comp. Biochem. Physiol. 50A: 753–757.

FRY, F. E., AND J. C. BUDD. 1958. The survival of yearling lake trout planted in South Bay, Lake Huron. Can. Fish Cult. 23: 9 p.

GAGE, S. H. 1929. Lampreys and their ways. Sci. Mon. 28: 401–416.

HANSON, L. H. 1972. An evaluation of selected marks and tags for marking recently metamorphosed sea lampreys. Prog. Fish-Cult. 34: 70–75.

HILE, R., P. H. ESCHMEYER, AND G. F. LUNGER. 1951a. Decline of the lake trout fishery in Lake Michigan. U.S. Fish. Wildl. Serv. Fish. Bull. 52: 77–95.

LAWRIE, A. H. 1970. The sea lamprey in the Great Lakes. Trans. Am. Fish. Soc. 99: 766–775.

LENNON, R. E. 1954. Feeding mechanism of the sea lamprey and its effect on host fishes. U.S. Fish. Wildl. Serv. Fish. Bull. 56: 247–293.

LOFTUS, K. H. 1958. Studies on river-spawning populations of lake trout in eastern Lake Superior. Trans. Am. Fish. Soc. 87: 259–277.

PYCHA, R. L., AND G. R. KING. 1975. Changes in the lake trout population of southern Lake Superior in relation to the fishery, the sea lamprey, and stocking, 1950–70. Great Lakes Fish. Comm. Tech. Rep. 28: 34 p.

SMITH, B. R., J. J. TIBBLES, AND B. G. H. JOHNSON. 1974. Control of the sea lamprey (*Petromyzon marinus*) in Lake Superior, 1953–70. Great Lakes Fish. Comm. Tech. Rep. 26: 60 p.

VAN OOSTEN, J. 1957. The skin and scales, p. 207–244. *In* M. E. Brown [ed.] The physiology of fishes. Vol. 1. Metabolism. Academic Press, Inc., New York, NY.

Predatory-Phase Sea Lampreys (*Petromyzon marinus*) in the Great Lakes[1]

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Incidentally caught predatory-phase sea lampreys were obtained from the commercial fisheries of the Laurentian Great Lakes, together with related catch data, in return for a reward offered to fishermen. Catches of sea lampreys per unit of fishing effort in Lake Superior generally paralleled other indices of sea lamprey abundance. Recently metamorphosed sea lampreys tended to appear early in the season in deepwater fisheries, typically those directed toward cisco (*Coregonus* spp.), whereas older specimens were taken more often in gear set at shallower depths during summer and fall. The proportion of male sea lampreys in the collections decreased annually between spring and fall, due apparently to a shoreward movement of the males. Large lake trout (*Salvelinus namaycush*) appeared to be the preferred prey of the sea lamprey. From studies of the stomach contents, sea lamprey feeding activity appeared to reach a peak in late summer or early fall, thereafter declining until the cessation of feeding in early spring. Growth rate reached a maximum in late summer or early fall. Greatest length was attained between January and March, after which a decrease in length was observed. Predatory-phase sea lampreys remained concentrated near the mouths of their parent streams if sufficient numbers of prey were present. Their distribution in the Great Lakes was related to the location of prey.

Key words: sea lamprey, predation, Great Lakes fishery

JOHNSON, B. G. H., AND W. C. ANDERSON. 1980. Predatory-phase sea lampreys (*Petromyzon marinus*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37: 2007–2020.

Grâce à un système de récompenses aux pêcheurs, nous avons pu obtenir des grandes lamproies marines dans la phase prédatrice, capturées fortuitement dans les pêches commerciales des Grands Lacs laurentiens, ainsi que les données de capture. En général, les prises de grande lamproie marine par unité d'effort dans le Lac Supérieur s'accordent avec d'autres indices d'abondance de cette espèce. Les lamproies récemment métamorphosées ont tendance à apparaître tôt dans la saison dans les pêches en eau profonde, typiquement celles visant les ciscos (*Coregonus* spp.), alors que les sujets plus âgés sont capturés plus souvent dans des engins tendus en eau moins profonde en été et en automne. La proportion des sujets mâles dans les collections diminue du printemps à l'automne, résultat, semble-t-il, d'une migration des mâles vers la rive. Les proies préférées de la grande lamproie marine semblent être les touladis (*Salvelinus namaycush*) de grande taille. Un examen des contenus stomacaux donne à croire que l'alimentation de la grande lamproie marine atteint un sommet à la fin de l'été ou au début de l'automne, pour ensuite diminuer jusqu'à un arrêt au début du printemps. Le taux de croissance atteint un maximum à la fin de l'été ou au début de l'automne. La longueur maximale est atteinte entre janvier et mars, après quoi on observe un rétrécissement. Les grandes lamproies marines dans la phase prédatrice demeurent concentrées près de l'embouchure de leur cours d'eau natal si les proies y sont présentes en nombre suffisant. Leur répartition dans les Grands Lacs est liée à celle des proies.

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LOFTUS and Regier (1972), summarizing the principal thesis of the Symposium on Salmonid Communities in Oligotrophic Lakes (SCOL), concluded that three major stresses — cultural eutrophication, overexploitation, and introduction of exotic species — led to the catastrophic declines in several valuable fish species in the Great Lakes, particularly the salmonids. Other SCOL participants (Christie 1972; Berst and Spangler 1972; Wells and McLain 1972; Lawrie and Rahrer 1972) documented the role played by the sea lamprey (*Petromyzon marinus*) as a factor in the declines of fish stocks in Lakes Ontario, Huron, Michigan, and Superior, respectively. The resulting crisis in the commercial fishing industry led to the development of the sea lamprey control program, under the Great Lakes Fishery Commission, as described by Smith et al. (1974). The implementation of sea lamprey control measures (electric barriers and selective toxicants), together with associated survey activities, provided in-investigators with opportunities to study the stream-dwelling larval stages and the anadromous spawning phase; however, the lake-dwelling predatory phase remained relatively unknown. Because the latter are frequently caught incidentally in the commercial fisheries of the Great Lakes, the Canadian agent of the Great Lakes Fishery Commission in 1967 initiated a system of rewards to commercial fishermen for collections of adult sea lampreys taken in commercial fishing gear, together with information on locations, dates, and methods of capture (Johnson 1969). A similar collection system was developed by the United States agent in 1969 (Great Lakes Fishery Commission 1970). This paper presents data from these two investigations.

Materials and Methods

Collections of predatory-phase sea lampreys, related catch records, and analysis of the data derived were conducted independently by the Great Lakes Fishery Commission's two control agents. Although attempts were made to collect similar data, some differences in information available and methods of collection occurred because of differences in the management and operations of the fisheries on opposite sides of the Great Lakes.

Cooperating fishermen were instructed, but not supervised, in collecting the material and recording the information; and were paid a reward of $1.00 per lamprey for the collection and preservation of specimens and related information. Specimens and data that appeared unreliable were not used in subsequent analyses. Although much of the catch information had to be accepted on faith, we believe that the information provided was accurate and reliable.

The following information was obtained: total length in millimetres, round weight in grams, sex, maturity (reported in Canada as immature, maturing, ripe, or spent; in the United States as recently metamorphosed $\leq$200 mm long, those >200 mm, and spawning-phase as described by Applegate 1950), condition of the gut (designated in Canada only as functional or not), fullness of the gut (described in Canada as full, partly full, trace, or empty; in the United States by the estimated percentage), contents of the gut (listed in Canada only as blood, eggs, both, or neither), and presence or absence of a tag.

Sea lampreys shrink in formalin. By comparing weights and lengths of specimens before and after preservation, it was determined that the change from the fresh condition is a nearly constant proportion of the given dimension. Since it may be assumed that most investigations of this kind would use preserved material, no attempt has been made to convert preserved measurements to fresh equivalents.

The following catch data supplied by fishermen were obtained: day, month, and year of capture; location, by statistical district of each lake (Smith et al. 1961); kind of fishing gear and mesh size as described by Hile (1962); depth of capture; target species (United States only); approximate length (United States only); and species of fish to which the lampreys were attached, or whether caught enmeshed; and identity of the fishermen.

Effort statistics provided by the Departments of Natural Resources of Michigan and Wisconsin to the United States control agent were used to determine catch-per-unit effort (CPE) of Lake Superior predatory-phase sea lampreys. In Canadian waters, however, CPE of sea lampreys could not be estimated reliably.

The kind of commercial fishing gear providing the largest number of sea lampreys varied among lakes as follows: large-mesh gill nets in Lake Superior; pound nets in Lake Michigan; trap nets (United States) and gill nets (Canada) in Lake Huron; trawls in Lake Erie; and hoop nets and beach seines in Lake Ontario. The primary target species of these fishing gears were: lake whitefish (*Coregonus clupeaformis*) and lake trout in Lake Superior; lake whitefish in Lakes Michigan and Huron; rainbow smelt (*Osmerus mordax*) in Lake Erie; and carp (*Cyrprinus carpio*) and bullhead (*Ictalurus* spp.) in Lake Ontario. Many sea lampreys also were captured by sport fishermen trolling for lake trout and salmon (*Oncorhynchus* spp.), and two predatory-phase sea lampreys attached to prey fish were captured at electrical barriers on the Brule and Two Hearted rivers.

Distribution and Abundance

OCCURRENCE IN THE FISHERIES

The collection of predatory-phase lampreys from the fisheries between 1967 and 1978 confirmed the predator's occurrence throughout Lakes Superior, Huron, Michigan, Erie, and Ontario, with the possible exception of Lake Erie's western basin. The size, number, or both, of predatory-phase sea lampreys captured in commercial fisheries may be attributed to many factors, including time of year, location, and depth of fishing, gear, mesh size, target species, seasonal changes in effort, and feeding habits of the sea lamprey. Larger sea lampreys were associated with gear of larger mesh in Lakes Superior, Michigan, and Huron (large-mesh vs. small-mesh gill nets: Table 1). In general, lengths of sea lamprey taken in impoundment gear were more broadly distributed than they were in enmeshing gear. The relatively large number of small lampreys taken by pound nets in Green Bay, which dominated the Lake Michigan collection (Table 1), is attributable to lack of access to deep water and absence of preferred prey,

TABLE 1. Number of predatory-phase sea lampreys collected by United States and Canadian fishermen combined, by length interval, and commercial fishing gear in the Great Lakes, 1967–78.

Length interval (mm)	Gill[a]					Type of net							
	A	B	C	D	E	Pound	Trap	Trawl	Drop	Fyke	Seine	Hoop	Trammel
						Lake Superior							
≤200		172	21			4	10						
201–249		100	21	2		11	17						
250–299		53	13	5		60	41						
300–349	2	65	66	12		116	51						
350–399	6	123	243	15		97	25						
400–449	16	163	524	12		83	17	2[b]					
450–499	15	56	304	4		34	8	3					
>499	3	15	43			5	1						
Total	42	747	1235	50		410	170	5					
						Lake Michigan							
≤200		164	60			816	95	8	2				
201–249		69	46			1105	153	29	1				
250–299		8	37			694	208	43					
300–349		4	53			311	162	94	1				
350–399		8	87			238	109	107	1				
400–449	1	20	128			401	62	132	2				
450–499	3	26	156			568	35	148	3				
>499	3	26	100	1		331	17	107	7	2			
Total	7	325	667	1		4464	841	668	17	2			
						Lake Huron							
≤200		280	77	11			66						
201–249		442	161	13	1	6	198						
250–299		352	368	40		6	307						
300–349		88	695	115		5	250						
350–399		41	793	186	2	1	196						
400–449		21	707	206	8	2	99						
450–499		8	419	137	9	3	55						
>499		1	237	39	18	2	21						
Total		1233	3457	747	38	25	1192						
						Lake Erie							
≤200		1					1				3		
201–249				2			3						
250–299				1				1					
300–349						1		3					
350–399						2		28					
400–449								73					
450–499						1	1	163			1		
>499								164			5	2	2
Total		1		3		4	5	432			9	2	2
						Lake Ontario							
≤200	1	41	14	3				1			6	2	
201–249		89	25	6			5				40	1	
250–299		124	110	30			12	4			127	5	
300–349		247	204	83			12	2			105	13	
350–399	4	397	377	139			22	3			74	74	
400–449	3	264	338	80			15	2			29	65	
450–499	6	107	143	82			2				17	32	
>499		59	73	79			3				6	5	
Total	14	1328	1284	502			71	12			404	197	

[a] Mesh sizes (stretched) in millimetres and (in parentheses) in inches — A = 25–60 (1–2⅜); B = 63–88 (2½–3½); C = 92–120 (3⅝–4¾); D = 124–200 (4⅞–7⅞); E = 203 (8).

[b] Lamprey taken by research personnel.

TABLE 2. Annual numbers of predatory-phase sea lampreys taken by United States and Canadian commercial fisheries of Lakes Superior, Huron, Michigan, Erie, and Ontario, 1967–78.

			Lake Huron								
	Lake Superior		Lake Proper		North Channel	Georgian Bay	Lake Michigan	Lake Erie	Lake Ontario	Totals	
Year	Canada	U.S.	Canada	U.S.	Canada	Canada	U.S.	Canada	Canada	Canada	U.S.
1967	73		1572		227	5		3	301	2181	
1968	35		1245		168	487		5	553	2493	
1969	24	118	918		371	138		117	1279	2847	118
1970	22	255	303	93	176	20	194	160	1815	2486	542
1971	29	639	367	202	137	3	1086	150	1089	1760	1927
1972	18	452	284	120	59	1	978	27	789	1178	1550
1973	15	390	78	39	71		730	3	47	214	1159
1974	20	225	35	22	88		647		115	258	894
1975	9	195	137	140	92		482		213	451	817
1976	34	167	194	130	74		404		13	315	701
1977		215		270			1355				1840
1978		118		329			202				649
Total	279	2774	5133	1345	1463	654	6078	465	6214	14,183	10,197

as more fully explained in the next section. The occurrence of large sea lampreys in the small-mesh fisheries for rainbow smelt in lakes Superior and Michigan, and yellow perch (*Perca flavescens*) in Lake Ontario, probably resulted from an association with large prey fish or movement of the lampreys into inshore waters before spawning. The large sea lampreys captured by trawlers fishing for alewife (*Alosa pseudoharengus*) in Lake Michigan were associated with incidental catches of large predators of alewife.

Many of the Canadian fishermen who contributed sea lampreys, reported approximately the same fishing effort throughout the study period (1967–76). Therefore numbers of sea lampreys collected (Table 2) can be taken as a rough estimate of their abundance, although they tend to overestimate the downward trends in abundance through time, as some fishermen stated that they ceased collecting sea lampreys as the abundance declined. The relative numbers collected annually from Lakes Superior and Huron are in general agreement with other measures of sea lamprey abundance such as the numbers caught at electrical barriers (Smith and Tibbles 1980). Lake Erie appeared to be an exception.

LAKE SUPERIOR

Fisheries in the Apostle Islands region consistently captured the largest number of sea lampreys collected in Lake Superior from 1969 to 1978. Forty-nine percent of the 2888 sea lampreys collected from the fisheries of Lake Superior came from this area. This corresponds to the fact that 53% of the spawning run sea lampreys taken at U.S. index electrical barriers from 1970 to 1978 came from nearby streams: the Brule and Amnicon rivers (Smith and Tibbles 1980).

Fisheries in the Keweenaw Peninsula area (MS-3) captured 103 (52%) of the recently metamorphosed sea lampreys ≤200 mm long, and of these, 92 (89%) were captured in small-mesh gill nets fishing for deepwater ciscoes (chubs) at an average depth of 123 m (range, 85–174). Applegate (1950) and Johnson (1969) made similar observations of recently metamorphosed sea lampreys captured in chub fisheries of Lake Huron.

LAKE MICHIGAN

Fifty-eight percent of the 4149 sea lampreys collected in Lake Michigan came from Green Bay, a quarter of these being small, recently metamorphosed individuals. Further, despite the confined nature of Green Bay, circumstantial evidence indicates that sea lampreys produced there contribute substantially to adjacent Lake Michigan proper (Smith and Tibbles 1980). The sharp reduction following the treatment of a single Green Bay tributary, the Peshtigo River (Wells 1980), supports this argument.

Most (84%) of the nearly mature spawning phase sea lampreys taken in Lake Michigan came from the pound net fishery of WM-4 close to the estuary of the Ahnapee River where they appear to have congregated in the manner observed much earlier in Lake Huron (Applegate 1950).

LAKE HURON

Fisheries in northern Lake Huron, including the western end of the North Channel, have consistently provided the majority of sea lampreys collected from this lake. Eighty-five percent of the U.S. collection came from statistical district MH-1, while 62 and 19%

of the Canadian collection came from statistical districts OH-1 and NC-1, respectively. Georgian Bay which in 1968 provided 35% of the Canadian Lake Huron total, yielded no sea lampreys after 1972.

Since 1977, increases in the number of lampreys captured from the fisheries, high scarring rates of fish, and large spawning runs of sea lampreys into tributaries of this lake and the St. Marys River (Braem et al. 1978) suggest a real increase in sea lamprey abundance in the waters of northern Lake Huron. Increasing catches of spawning run sea lamprey since 1973 at the electric barrier on Kaskawong River (a tributary to NC-1) support this contention (Smith and Tibbles 1980).

LAKE ERIE

Almost the entire Lake Erie collection of 465 sea lampreys came from trawl fisheries conducted in statistical district OE-4 in depths of 20–40 m. A small number were taken in hoop-nets set at shallower depths in the same statistical district. Fishermen reported that the lampreys were taken in association with incidental catches of whitefish. Four of the six known sea lamprey streams on the Canadian side empty into the eastern basin of Lake Erie (Pearce et al. 1980).

LAKE ONTARIO

Ninety-five percent of the Lake Ontario collection of 6214 sea lampreys came from statistical district 00-3 (that part of the lake adjacent to Prince Edward Co.). Most of them were taken in shallow inshore waters by gill net and trap net fishermen whose catches consisted mainly of lake whitefish, yellow perch, carp, suckers (*Catastomus* spp.), northern pike (*Esox lucius*), and bullheads. Although sources of sea lamprey are widely distributed around Lake Ontario (Pearce et al. 1980), commercial fishing in recent years has been concentrated in the eastern end (Christie and Kolenosky 1980). The inauguration of sea lamprey control measures in 1971 and subsequent increases in the plantings of salmonids (Pearce et al. 1980) not only reduced sea lamprey abundance but probably caused a shift in predation of the residual predators away from the commercially fished species.

DEPTH DISTRIBUTION

Sea lampreys from the Great Lakes commercial fishery revealed no depth limitations per se to their distribution: they occurred wherever their prey were caught. The observed variations between lakes in depth distribution of sea lampreys (Fig. 1) tended to correspond to the relative amounts of fishing effort at those depths in the respective lakes as reported by participating fishermen. For example, in Lake Ontario the reason for the apparent concentration of specimens in the shallowest interval (0–19 m deep) is that most of the collections were obtained from shallow inshore fisheries, whereas in lakes Superior and Huron, the collections of sea lampreys extended from all depths down to 100-183 m, although in these two lakes most fishing occurred, and most lampreys were collected, at depths less than 40 m. In Lake Michigan sea lampreys were recovered at depths ranging from 2 to 143 m, although most commonly, depending on the season, at depths between 2 and 39 m.

The changes observed in sea lamprey depth distribution indicated an initial dispersal of recently metamorphosed adults entering the lake in the fall, winter, and early spring primarily to the deeper waters; followed by a shift to inshore waters starting in early summer and persisting until the following spring when the final spawning migration into the streams occurs: these observations support the earlier work of Applegate (1950). Sixty-three percent of recently metamorphosed sea lampreys ($\leq$200 mm) were captured by deepwater cisco fisheries at depths greater than 79 m in Lake Superior and greater than 59 m in Lake Michigan proper. Of the lampreys <251 mm long, 415 (49%) were captured in deepwater areas; whereas of those $\geq$251 mm long, 4417 (92%) were captured in shallow inshore waters (Fig. 2). The numbers of lampreys collected in deepwater areas show a sharp decrease between the lengths of 200 and 251 mm, indicating that there is a systematic change in the bathymetric distribution of sea lampreys of this size. Sea lampreys of this length range (200–251 mm) were most often captured by the fisheries during November–July (Fig. 3).

Commercial Fishing Gear Statistics

Sea lampreys captured in large-mesh gill nets were larger on the average than those captured in pound nets or small-mesh gill nets. In Lake Superior large-mesh gill nets were fished principally for lake whitefish at an average depth of 37 m (range, 4–146), small-mesh gill nets for deepwater cisco spp. and lake herring (*Coregonus artedii*) at 112 m (range, 8–164), and pound nets for lake whitefish at 18 m (range, 2–24). Mean lengths of sea lampreys caught in large-mesh gill nets, pound nets, and small-mesh gill nets were 423, 324, and 315 mm, respectively. A similar difference was observed in the Lake Huron fisheries (Johnson 1969).

Large-mesh gill nets captured four times as many sea lampreys as small-mesh gill nets; the size and species of fish probably contributing to this difference. The number of sea lampreys per 30 480 m (100 000 feet) of gill net of large- and small-mesh were 2.08 and 0.49, respectively. For pound nets the CPE was 0.07 sea lamprey per lift. For large-mesh gill nets, the period from December through May accounted for 46% of the effort and 93% of the lampreys (Fig. 4); whereas increasing effort from April through June showed decreasing numbers of large mature lampreys captured, suggesting that sea lampreys left the areas of

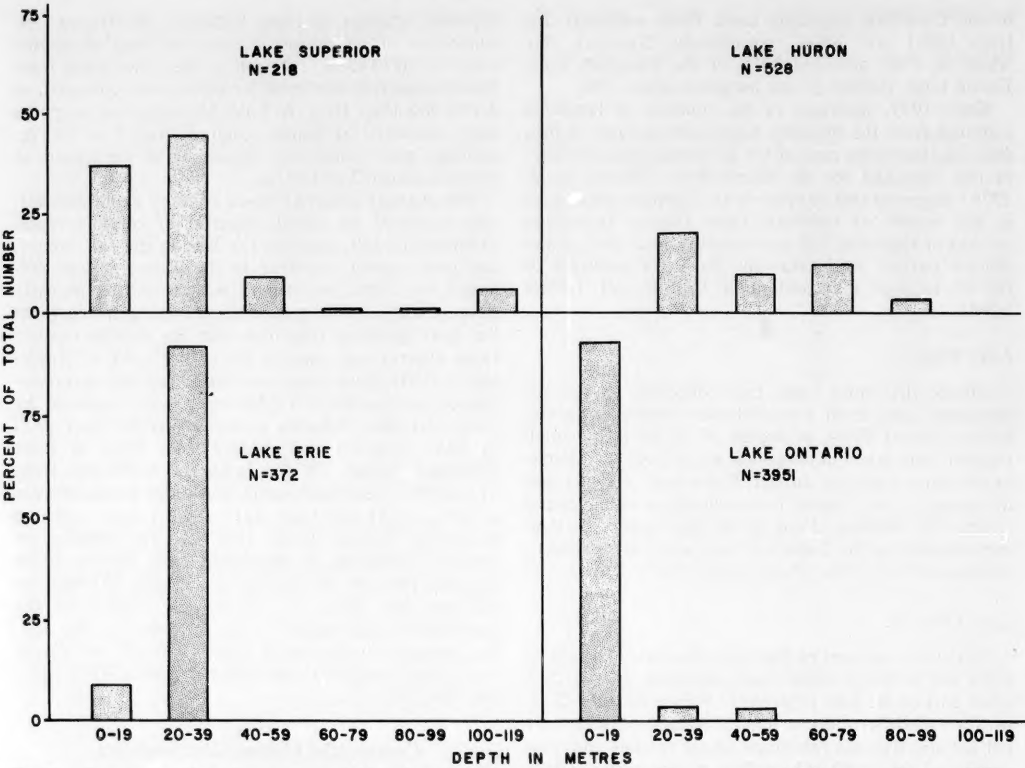

FIG. 1. Percentage of sea lamprey caught in selected depth intervals by Canadian commercial fishermen: all years 1967–76 combined.

commercial fishing activity to begin their spawning migrations. For small-mesh gill nets, from December through May, 34% of the total effort accounted for 61% of the lampreys, which include a large number of recently metamorphosed sea lampreys. For pound nets, from May through October, the percentage of effort was similar to the percentage of lampreys captured, which consisted almost entirely of the young adult population (Fig. 4).

CATCH-PER-UNIT OF EFFORT VS. ELECTRICAL BARRIER CATCH

Catch-per-unit of effort of sea lampreys caught incidentally in the commercial fisheries of the Great Lakes may be a reliable method to monitor relative abundance of sea lamprey populations. For the period from 1970 to 1978, sea lamprey catch data from the electrical barriers on Lake Superior yielded a significant correlation with the CPE of predatory-phase sea lampreys collected from large- and small-mesh gill nets in United States waters during the biological year (June–May) preceding the barrier catch ($r = 0.822$, $P = 0.01$) (Fig. 5). The correlations for large-mesh and small-mesh gill nets alone were also significant ($r = 0.806$, $P = 0.01$; $r = 0.674$, $P = 0.05$, respectively). For impoundment gear, which was limited to one statistical district (Wisconsin), and probably did not represent the lake population in its entirety, there was no significant correlation.

Biological Characteristics

SEX RATIOS IN PREDATORY- VS. SPAWNING-PHASE SEA LAMPREYS

In nearly all collections from the commercial fisheries of the two countries, female predatory-phase sea lampreys outnumbered males confirming Johnson's (1969) report of similarly lop-sided sex ratios. Only once in the period 1967–76 (Lake Ontario in 1973) did the percentage of males in any of the Canadian samples

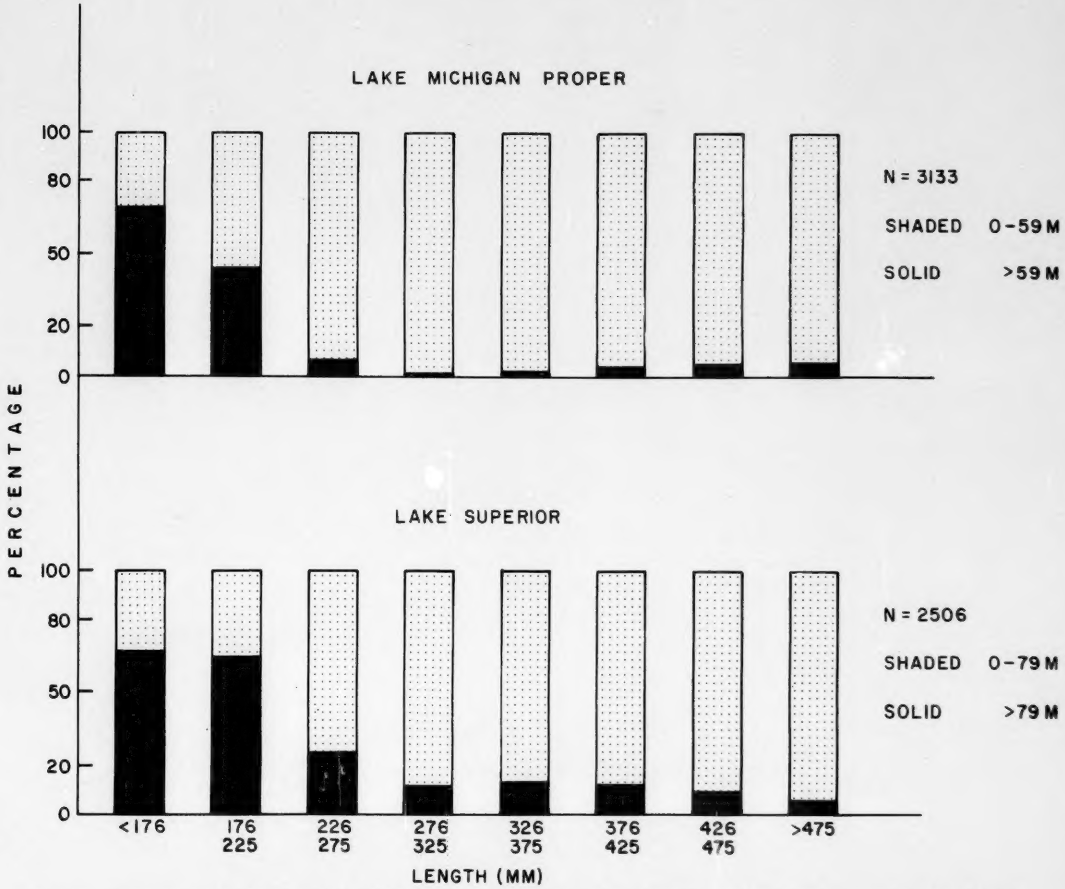

FIG. 2. Percentage of predatory-phase sea lampreys by length interval (mm) from two depth zones in Lake Superior (1969–78) and Lake Michigan proper (1970–78).

from Lakes Superior, Huron, Erie, or Ontario exceed 50% (Fig. 6) although there does appear to have been a general increase in male:female ratios towards the end of the period. Generally similar sex ratios characterized samples from United States waters of Lake Superior (1970–78) and of Lakes Michigan and Huron (1971–78) as well (Table 3). Moreover, these values were about 8% less than those observed in spawning-phase sea lampreys taken in the tributaries of each lake (Table 3) suggesting that males were not fully available to these commercial fisheries for some reason or that females were more vulnerable. Johnson (1969) has suggested the possibility of sex segregation and Parker and Lennon (1956) that females feed more often and longer and hence are more susceptible to capture.

VARIABILITY OF SEX RATIOS

For predatory-phase sea lampreys, a segregation of the sexes develops in the spring or early summer, the females seeking deeper offshore waters (where they encounter gill net sets), whereas the males tend to move inshore (where they may be taken in seine hauls). The percentage of male sea lampreys decreased from spring or early summer through the autumn for most of the lakes (Fig. 7), except for Lake Erie, where the lowest percentage of males occurred in September. The overall percentage of males for all months combined in Lakes Superior, Huron, and Ontario showed remarkable consistency at 10 or 11%. Again, Lake Erie was the exception with an overall figure of 20% males.

In the United States fisheries of Lakes Superior,

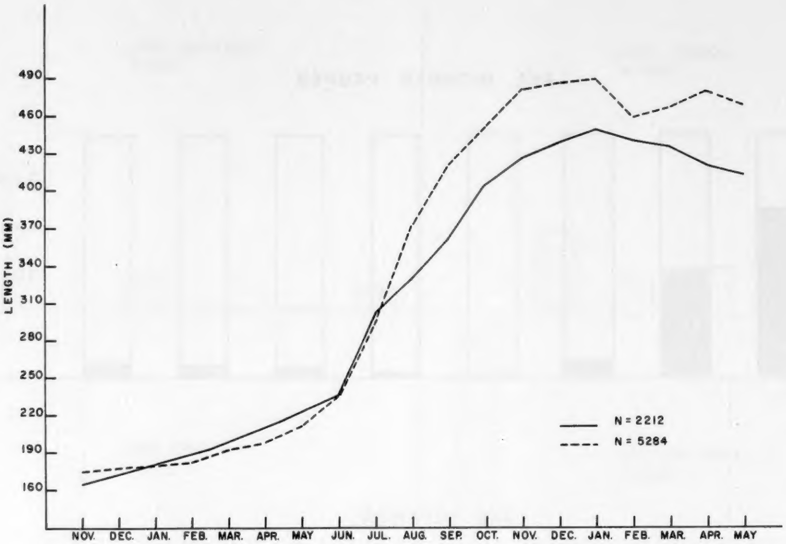

FIG. 3. Average length of predatory-phase sea lampreys in Lake Superior, 1969–75 (solid line), and Lake Michigan, 1970–76 (dashed line).

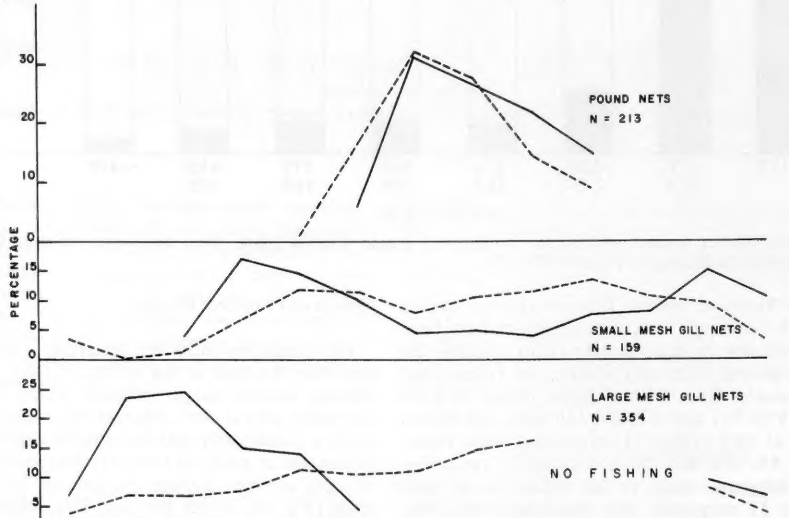

FIG. 4. Percentage of predatory-phase sea lampreys captured (solid line), and percentage of effort (dashed line) for large- and small-mesh gill nets and pound nets in Lake Superior, 1971–74.

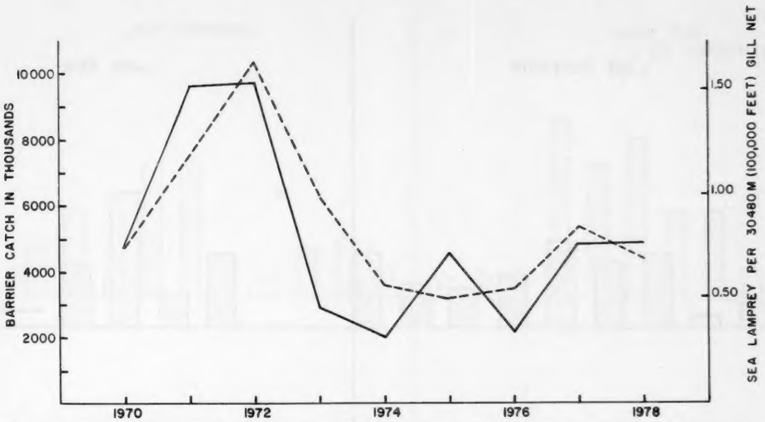

FIG. 5. Comparison of the catch of predatory-phase sea lampreys per 3248 m (100 000 ft) of gill net (dashed line), and the number of spawning-phase sea lampreys taken at the electrical barriers on Lake Superior, 1970–78 (solid line).

TABLE 3. Difference in percentage males of spawning-phase,[a] and predatory-phase[b] sea lampreys from Lake Superior, 1970–78, and Lakes Michigan and Huron, 1971–78.

	Superior		Michigan		Huron	
Phase	Sample size	% males	Sample size	% males	Sample size	% males
Spawning	36 522	31.1	6275	42.6	4707	39.4
Predatory	2800	22.7	7082	34.5	1351	30.9
Difference		8.4		8.1		8.5

[a] Spawning-phase sea lampreys collected at United States electric barriers on Lakes Superior and Huron and from mechanical traps on Lakes Michigan and Huron.

[b] Predatory-phase sea lampreys collected from United States commercial fishermen.

Michigan, and Huron the percentage of males decreased during the predatory-phase of life, from 31.4, 36.6, and 38.0%, respectively, for those ≤200 mm long, to 13.6, 30.5, and 24.5%, respectively, for those >499 mm long (Table 4).

Differences in sex ratio occurred also with different types of fishing gear. In Lakes Superior and Erie numbers were insufficient to yield meaningful comparisons between gears. In Lake Huron sea lampreys from gill net catches (offshore) were only 10% males, whereas those from trap nets (inshore) were 20% males. In Lake Ontario sea lampreys from gill nets were 9% males whereas those from seines were 24% males. These differences are significant at the 1% level of probability.

PREY-HOST RELATIONSHIPS

Lake trout, the preferred prey of the sea lamprey because of its large size and occurrence in the colder regions of the lakes (Aron and Smith 1971), is regaining its former abundance through massive plantings in the Great Lakes. Of the 1615 predatory-phase sea lampreys captured for which host species was determined, 59% were attached to lake trout (Table 5). The most significant exception was 67 (55%) sea lampreys ≤200 mm long which were attached to cisco. This apparent preference for a prey species may in fact be a depth-dependent phenomenon related to a temperature preference of the predator at a time of the year when the warmest water is at great depth.

Sea lampreys preferred large lake trout over smaller ones. Sea lampreys ≥250 mm long were attached to lake trout between 507 and 684 mm (20.0–26.9 inches) long most frequently (70% of all attachments), whereas those <250 mm were generally attached to cisco or lake herring. The low occurrence of attachments on lake trout <457 mm (18 inches) long probably reflects a preference for prey size, whereas the low number of attachments on lake trout >684 mm (26.9 inches) long may reflect the small number of lake trout surviving to that size. Comparable size preferences

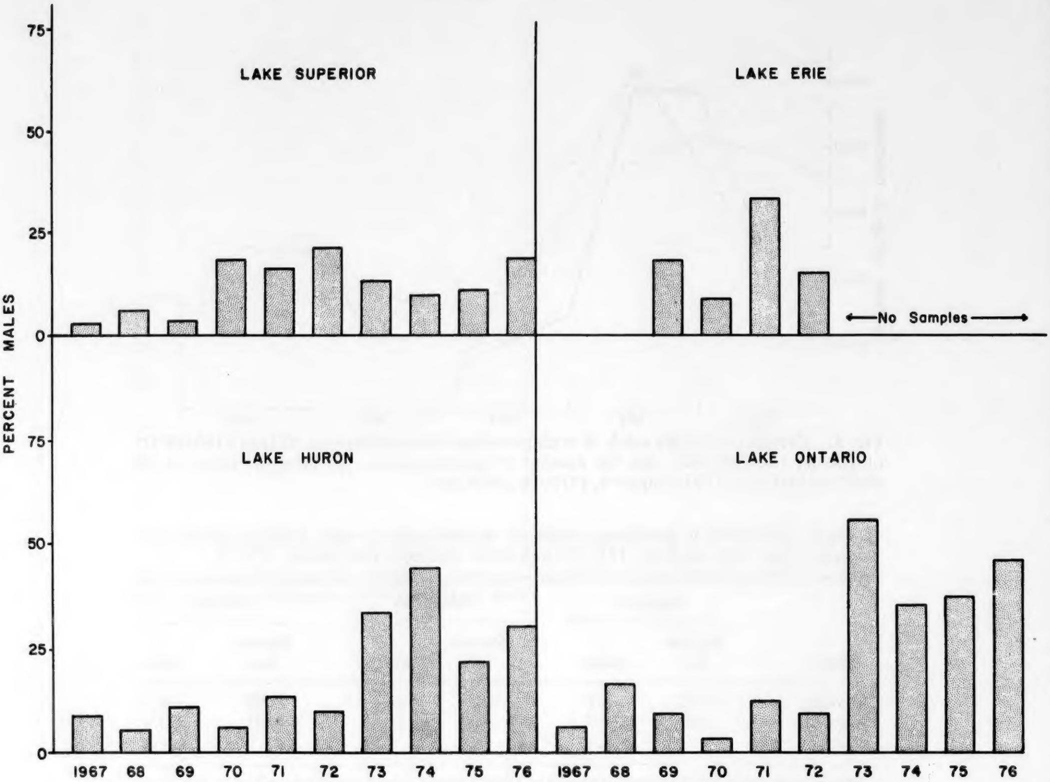

FIG. 6. Percent males in annual catches of adult sea lampreys by Canadian commercial fishermen, 1967–76.

TABLE 4. Percentage males of predatory-phase sea lampreys by length interval, Lake Superior, 1969–78, and Lakes Michigan and Huron, 1970–78.[a]

Length interval (mm)	Superior		Michigan		Huron	
	No. in sample	% males	No. in sample	% sample	No. in sample	% males
≤200	194	31.4	1148	36.6	71	38.0
201–249	139	34.5	1417	37.2	207	29.4
250–299	207	30.9	1001	34.2	319	34.4
300–349	369	27.1	629	38.7	262	31.6
350–399	549	22.5	561	32.7	209	30.1
400–449	835	19.4	761	30.2	131	29.0
450–499	441	15.4	957	32.4	99	23.2
>499	66	13.6	608	30.5	53	24.5
Total	2800		7082		1351	
Average		22.7		34.5		30.9

[a] United States collections.

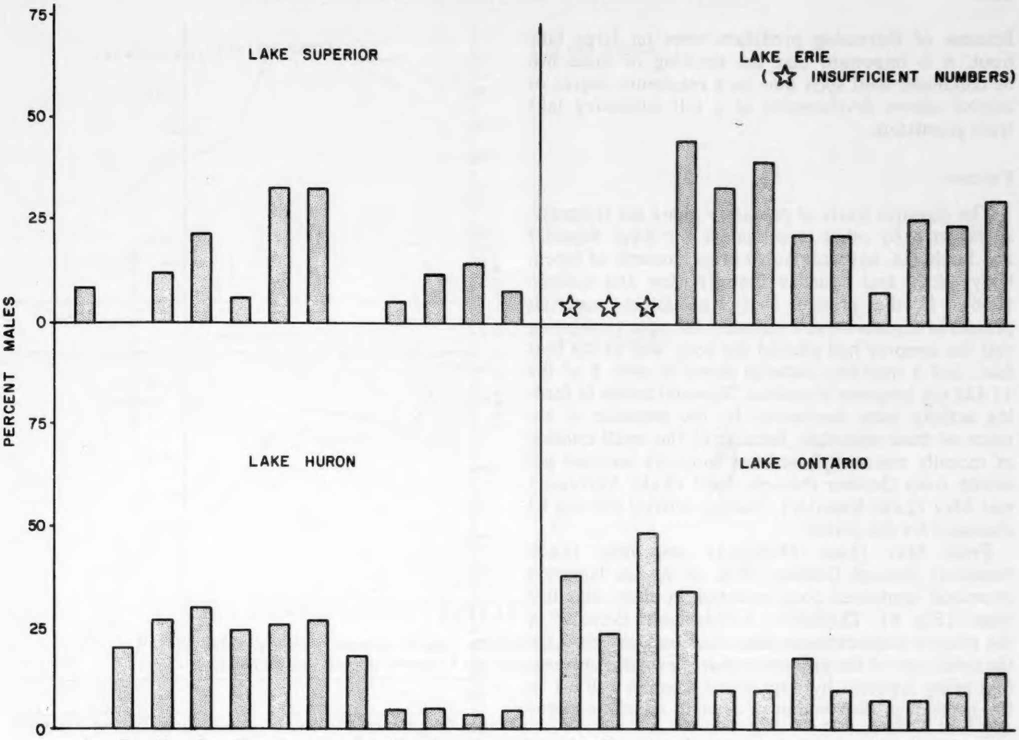

FIG. 7. Percent males in monthly catches of adult sea lampreys by Canadian commercial fishermen, 1967–76 combined.

TABLE 5. Number of predatory-phase sea lampreys by length interval attached to host species, Lake Superior, 1969–78.[a]

	Lamprey length (mm)								
Host species	≤200	201–249	250–299	300–349	350–399	400–449	450–499	>499	Total
Lake trout	17	25	57	113	217	345	167	15	956
Lake whitefish		4	1	13	44	130	86	20	298
Lake herring	35	24	13	19	37	38	12	3	181
Cisco spp.	67	27	9	3	8	14	3	1	132
Burbot			2	1	1	7	8	1	20
Sucker spp.					4	7	7		18
Rainbow trout	2		1				1		4
Brown trout				1	1				2
Round whitefish	1					1			2
Northern pike			1						1
Coho salmon			1						1
Total	122	80	85	150	312	542	284	40	1615

[a]United States collections; for accuracy of data, only sea lampreys captured in gill nets, sport fishing, and trolling were used.

have been reported by other investigators who correlated scarring rates with size of fish: lake trout (Wigley 1959; Budd et al. 1969); white suckers, *Catostomus commersoni* (Hall and Elliott 1954; Coble 1967); rainbow trout, *Salmo gairdneri* (Berst and Wainio 1967); splake, *Salvelinus fontinalis* × *S. namaycush* (Berst and Spangler 1970); and lake trout, white sucker, splake, and carp (Farmer and Beamish 1973).

Because of increasing predation rates on large lake trout, it is important that the stocking of these fish be continued until such time as a maximum degree of control allows development of a self sustaining lake trout population.

FEEDING

The digestive tracts of predatory phase sea lampreys, as reported by other investigators for lakes Superior and Michigan, have contained large amounts of blood, body juices, and liquefied flesh (Parker and Lennon 1956). In the present study, additional materials present in digestive tracts included fish eggs (indicating that the lamprey had pierced the body wall of the host fish) and a mud-like material found in only 2 of the 11 428 sea lampreys examined. Seasonal trends in feeding activity were determined by the presence or absence of these materials. Because of the small number of recently metamorphosed sea lampreys sampled per month from October through April (Lake Michigan) and May (Lake Superior), feeding activity will not be discussed for this period.

From May (Lake Michigan) and June (Lake Superior) through October, 70% of the sea lampreys examined contained food material in their digestive tracts (Fig. 8). Thereafter, a continuous decrease in the relative number containing food was observed for the remainder of the predatory-phase, a similar observation being reported by Parker and Lennon (1956) in the percentage distribution of feeding attacks on prey fish.

We observed feeding activity to be related to rate of growth as indicated by the increase in mean length in the predatory-phase of the sea lamprey. A significant correlation existed between the percentage of lampreys with food material in their digestive tracts and the percentage increase in length in Lake Michigan ($r = 0.743$, $P < 0.01$). The correlation for Lake Superior was also significant ($r = 0.738$, $P = 0.05$).

GROWTH RATE

Newly transformed sea lampreys migrate downstream in late fall and early spring (Applegate 1950). Spawning, followed quickly by death, usually occurs in May or June of the second year, resulting in an average duration of adult life of 18 mo. Therefore from the fall to the following spring, two age-groups of predatory-phase sea lampreys may occur in the Great Lakes, while for the remainder of the year only one age-group is present. We have not found newly transformed sea lampreys in the fishery earlier than October, nor encountered many spawning-phase sea lampreys in the fishery later than June. For the Canadian data, in calculating mean lengths (Fig. 9) and weights of sea lampreys at monthly intervals through the year we segregated the two age-classes in all months in which they occurred, and calculated the mean lengths separately, according to the sea lamprey's "biological" adult life span which begins as early as October and ends before July of the second following year. Since there were no consistent size differences between male and female sea lamprey at the same period, the sexes were combined.

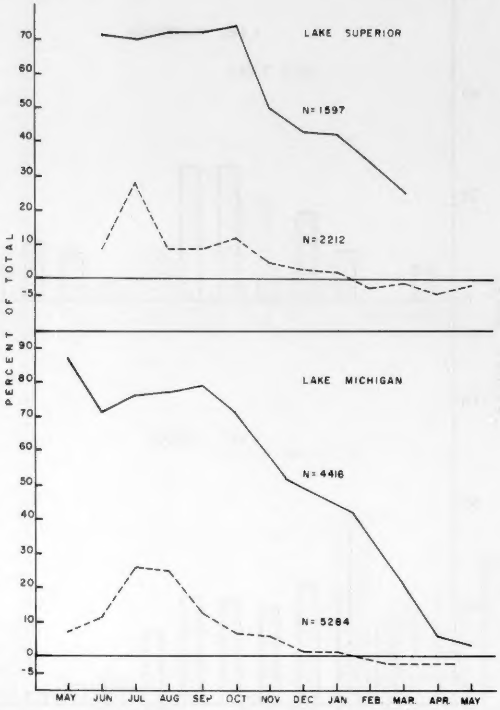

FIG. 8. Percentage of predatory-phase sea lampreys with food in the digestive tract (solid line), and percentage of growth in length (dashed line) in Lake Superior, 1969–76, and Lake Michigan, 1970–75.

These data (Fig. 9) indicate that increases in mean length of sea lampreys were irregular. For the most part, these irregularities were artifacts of the collection methods and probably reflected unequal representation, from one interval to the next, of groups of sea lampreys associated with different segments of the fishery. The size differences were probably caused by dietary or environmental factors, or both, which the predators encountered. The greatest increase in mean weight of sea lampreys occurred generally during the early fall of the first year of adult life. The lampreys reached their greatest mean length and weight in April or May of the second year of adult life. Subsequently, the mean length and weight decreased slightly. This decrease may be due to actual shrinkage of the animals

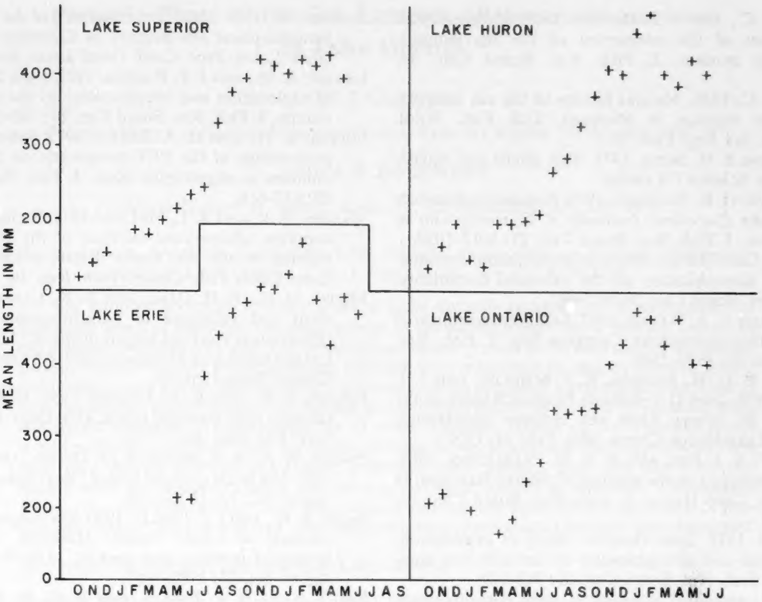

FIG. 9. Monthly mean lengths of sea lampreys caught in the Canadian commercial fishery, 1967–76. The two age groups present from October through June have been segregated.

after the cessation of feeding prior to spawning. It may also be the result of a gradual withdrawal of the larger specimens from the prey population, since the earliest spawning migrants are generally larger than subsequent members of the spawning runs.

These data also indicate that sea lampreys in Lake Erie were, on the average, larger than those in any other lake for the same month and in comparable age-groups. Although no reason for this difference can be advanced with certainty, it is possible that dietary constraints were not a controlling factor in the Lake Erie sea lamprey population; but that other factors, the most obvious of which is environmental, limited the population size.

Growth in length for recently metamorphosed sea lampreys from the United States waters of lakes Superior and Michigan was slow. Between November and June, for the first year of life, mean lengths increased from 165 mm in Lake Superior and 176 mm in Lake Michigan to 236 mm for both lakes (Fig. 3). Applegate (1950) observed a similar slow rate of growth of recently metamorphosed sea lampreys from Lake Huron. From June through January, rate of growth increased rapidly, as shown by increases in mean lengths from 236 to 447 mm in Lake Superior and to 487 mm in Lake Michigan. Maximum size was attained during January in both lakes, but as demonstrated by the growth curves, lampreys grew faster, and reached a mean length 40 mm greater in Lake Michigan. During the remaining 5-mo period (January-May), and before the spawning migrations, average length decreased, as it did in collections from Canadian waters. Similar decreases were observed by Anderson and Manion (1977) in the thickness of the dermal layer of lampreys from January through May. It is generally accepted that some shrinkage or decrease in the length occurs during the spawning migration (Wigley 1959; Manion and McLain 1971; Moore et al. 1974).

We may now generalize that sea lampreys entering the Great Lakes, following metamorphosis in late fall through spring, grow slowly in length until summer, rapidly increase their growth until early fall, reach maximum size about January, then gradually decrease in length until spawning (Parker and Lennon 1956).

Acknowledgments

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Anderson, W. C., and P. J. Manion. 1977. Morphological development of the integument of the sea lamprey, *Petromyzon marinus*. J. Fish. Res. Board Can. 34: 159–163.

Applegate, V. C. 1950. Natural history of the sea lamprey, *Petromyzon marinus*, in Michigan. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. 55.

Aron, W. I., and S. H. Smith. 1971. Ship canals and aquatic ecosystems. Science 174 (4004).

Berst, A. H., and G. R. Spangler. 1970. Population dynamics of F_1 splake (*Salvelinus fontinalis* × *S. namaycush*) in Lake Huron. J. Fish. Res. Board Can. 27: 1017–1032.

1972. Lake Huron: effects of exploitation, introductions and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 877–887.

Berst, A. H., and A. A. Wainio. 1967. Lamprey parasitism of rainbow trout in southern Georgian Bay. J. Fish. Res. Board Can. 24: 2539–2548.

Braem, R. A., B. G. H. Johnson, R. J. Schuldt, and J. J. Tibbles. 1978. Joint U.S.–Canada Progress Report on the status of St. Marys River sea lamprey populations. G.L.F.C. Lake Huron Comm. Mtg. Feb. 21, 1979.

Budd, J. C., F. E. J. Fry, and P. S. M. Pearlstone. 1969. Final observations on the survival of planted lake trout in South Bay, Lake Huron. J. Fish. Res. Board Can. 26: 2413–2424.

Christie, W. J. 1972. Lake Ontario. effects of exploitation, introductions and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 913–929.

Christie, W. J., and D. P. Kolenosky. 1980. Parasitic phase of the sea lamprey (*Petromyzon marinus*) in Lake Ontario. Can. J. Fish. Aquat. Sci. 37: 2021–2038.

Coble, D. W. 1967. The white sucker population of South Bay, Lake Huron, and effects of the sea lamprey on it. J. Fish. Res. Board Can. 24: 2117–2136.

Farmer, G. J., and F. W. H. Beamish. 1973. Sea lamprey (*Petromyzon marinus*) predation on freshwater teleosts. J. Fish. Res. Board Can. 30: 601–605.

Great Lakes Fishery Commission. 1970. Annual Report for the year 1969. Ann Arbor, Mich.

Hall, A. E., Jr., and O. R. Elliott. 1954. Relationship of length of fish to incidence of sea lamprey scars on white suckers, *Catostomus commersoni*, in Lake Huron. Copeia 1: 73–74.

Hile, R. 1962. Collection and analysis of commercial fishery statistics in the Great Lakes. Great Lakes Fish. Comm. Tech. Rep. 5.

Johnson, B. G. H. 1969. Some statistics of the populations of parasitic-phase sea lamprey in Canadian waters of the Great Lakes. Proc. Conf. Great Lakes Res. 12: 45–52.

Lawrie, A. H., and J. F. Rahrer. 1972. Lake Superior effects of exploitation and introductions on the salmonid community. J. Fish. Res. Board Can. 29: 765–776.

Loftus, K. H., and H. A. Regier. 1972. Introduction to the proceedings of the 1971 symposium on salmonid communities in oligotrophic lakes. J. Fish. Res. Board Can. 29: 613–616.

Manion, P. J., and A. L. McLain. 1971. Biology of larval sea lampreys (*Petromyzon marinus*) of the 1960 year class, isolated in the Big Garlic River, Michigan, 1960–65. Great Lakes Fish. Comm. Tech. Rep. 16.

Moore, H. H., F. H. Dahl, and A. K. Lamsa. 1974. Movement and recapture of parasitic-phase sea lampreys (*Petromyzon marinus*) tagged in the St. Marys River and Lakes Huron and Michigan, 1963–67. Great Lakes Fish. Comm. Tech. Rep. 27.

Parker, P. S., and R. E. Lennon. 1956. Biology of the sea lamprey in its parasitic phase. U.S. Dept. Int. Fish Wildl. Serv. Res. Rep. 44.

Pearce, W. A., R. A. Braem, S. M. Dustin, and J. J. Tibbles. 1980. Sea lamprey in the Lower Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1802–1810.

Smith, B. R., and J. J. Tibbles. 1980. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936–78. Can. J. Fish. Aquat. Sci. 37: 1780–1801.

Smith, B. R., J. J. Tibbles, and B. G. H. Johnson. 1974. Control of the sea lamprey, *Petromyzon marinus*, in Lake Superior, 1953–70. Great Lakes Fish. Comm. Tech. Rep. 26.

Smith, S. H., H. J. Buettner, and R. Hile. 1961. Fishery statistical districts of the Great Lakes. Great Lakes Fish. Comm. Tech. Rep. 2.

Wells, L. 1980. Lake trout (*Salvelinus namaycush*) and sea lamprey (*Petromyzon marinus*) populations in Lake Michigan, 1971–78. Can. J. Fish. Aquat. Sci. 37: 2047–2051.

Wells, L., and A. L. McLain. 1972. Lake Michigan: effects of exploitation, introductions and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 889–898.

Wigley, R. L. 1959. Life history of the sea lamprey of Cayuga Lake, New York. U.S. Fish Wildl. Serv. Fish. Bull. 59 (154): 561–617.

Parasitic Phase of the Sea Lamprey (*Petromyzon marinus*) in Lake Ontario[1,2]

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Sea lamprey produced in other areas of Lake Ontario appeared to be responsible for significant levels of predation on target species of the eastern outlet basin. The life history of the lamprey is simple with only one parasitic generation present in the lake during the feeding period. Wound frequencies on gillnetted whitefish were influenced by season, fish size, gillnet set duration, and a large random error component which suggested a contagious distribution. Scar frequencies were influenced by fish age and indicated improved survival of whitefish when fish weight exceeded lamprey weight by 43 times. Lamprey impact on the whitefish stocks would probably have been more important at lower fishing intensities. The lamprey may have been prey limited, and size and species preference were probably such that lake trout and burbot were not buffered against sea lamprey by white suckers or whitefish. The analysis favored the view that lamprey were innocuous in 19th century Lake Ontario by reason of prey size and density, but climatic and other environmental effects could also have been important.

Key words: sea lamprey, lake whitefish, Lake Ontario

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Les grandes lamproies marines provenant d'autres régions du lac Ontario semblent être responsables d'une importante prédation sur les espèces cibles du bassin de l'effluent est. Le cycle biologique de la lamproie est simple, une seule génération parasitaire étant présente dans le lac durant la période d'alimentation. La fréquence des blessures sur des grands corégones capturés au filet maillant est affectée par la saison, la taille du poisson, la durée de séjour dans l'eau du filet et une importante erreur aléatoire laissant croire à une distribution contagieuse. La fréquence des cicatrices est affectée par l'âge du poisson et indique une meilleure survie des grands corégones quand le poids de ces derniers est de 43 fois ou plus supérieur à celui des lamproies. L'impact de la grande lamproie marine sur les stocks de grands corégones serait probablement plus marqué à des intensités de pêche plus faibles. Il est possible que la grande lamproie marine soit limitée par les proies. Le choix des tailles et des espèces est probablement tel que le meunier noir ou le grand corégone ne peuvent servir de tampon contre la grande lamproie marine pour le touladi et la lotte. Cette analyse semble appuyer la thèse que cette lamproie était inoffensive dans le lac Ontario au XIXe siècle à cause de la taille et de la densité des proies, mais le climat et autres effets de l'environnement ont pu être aussi des facteurs importants.

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THE sea lamprey (*Petromyzon marinus*) of Lake Ontario occupies a place of special interest in the general context of the Great Lakes sea lamprey problem. There is little doubt that Lake Ontario was the reservoir which supplied the colonists that ultimately proliferated in the upper Great Lakes. The explosive impact of these colonizations is in contrast with the Lake Ontario situation where the lamprey was not an obvious threat to the prey stocks until recent historic times. This suggests either natural control over lamprey numbers or some form of accommodation between predator and prey, and either possibility has significance for sea lamprey abundance control efforts (Christie 1974). In this paper the available evidence relevant to these questions is reviewed.

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[1] This paper forms part of the Proceedings of the Sea Lamprey International Symposium (SLIS) convened at Northern Michigan University, Marquette, Michigan, July 30–August 8, 1979.

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The longest continuous observational series concerned the interactions between lamprey and lake whitefish (*Coregonus clupeaformis*) and this spanned the years 1954–72. The whitefish data collection actually began in 1944 and it is thought significant that project workers before 1953 did not regard lamprey wounding as sufficiently important to record. A number of papers (Lapworth 1956; Christie 1963, 1968; Christie and Regier 1973) have dealt with the eastern Lake Ontario whitefish data series, but the role of the lamprey in the dynamics of these stocks has not previously been analyzed. The data set is comprehensive, moreover, and on this account it permitted study of some of the sources of variability in sea lamprey wound and scar statistics, and these analyses also form part of this work.

Materials and Methods

We deal briefly with the known history of the sea lamprey in Lake Ontario, but the quantitative analysis is concentrated on observations made during the past 25 yr. Even for the recent period, the record is deficient because the research activities of the Ontario Department of Lands and Forests (Ontario Ministry of Natural Resources since 1972) were confined to the eastern end of the lake, and more importantly, because the sequence of fish species changes in Lake Ontario (Christie 1972) acted to break the continuity of observations on lamprey predation activity.

The record is most incomplete with respect to the U.S. side of Lake Ontario. There has been no open lake commercial fishery of consequence there for many years so no observations comparable to those made in the Canadian waters was possible. More recently, this situation was corrected by means of intensive lakewide fish stock monitoring activities undertaken by both the U.S. Fish and Wildlife Service, and the New York Department of Environmental Conservation. These efforts will make it possible to assess future changes in the lamprey stocks, on a lakewide international basis, but for the present report, it was not necessary to draw on the recent U.S. observations.

In addition to the data obtained through sampling the summertime catch of the eastern Lake Ontario whitefish fishery, information concerning sea lamprey predation was accumulated in the course of routine gillnetting and trap netting within the Bay of Quinte, and through examination of lake trout produced by an experimental planting program in the east end of the lake during the late 1950s and early 1960s. From 1954 to 1963 commercial fishermen were asked to report lamprey wounding and scarring frequencies on all species caught on a specified day each month. Although incomplete, these reports are the only information source from the small fisheries of central and western Lake Ontario.

Although whitefish stocks were no longer present in commercial abundance when the sea lamprey control program began in 1971, observations on coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) stocked before and after 1971, were useful in evaluating the success of the program. Results from salmon returning to the Credit River (Ontario) are examined.

Wounds on fish taken in the open lake waters were always considered to be lesions resulting from attacks by sea lamprey. The only other lamprey which is known from Lake Ontario, and has a parasitic phase, is the silver lamprey (*Ichthyomyzon unicuspis*). This species is limited to a few streams at the west end of the lake, attacks nearshore prey, produces small lesions, and is not generally considered abundant in the lake (Crossman and Van Meter 1979). Of the many lampreys collected in the course of this investigation, moreover, all were sea lamprey.

The Lake Ontario research group has always considered a fresh wound as one which has not yet achieved a smooth glossy surface. Typically, wounds are rough on the surface and raw-appearing – often with fluid loss still in evidence after the fish has surficially dried. Scars, of course, become progressively less distinguishable as indications of sea lamprey attacks as the original wounds lose shape and size, and as pigmentation redevelops near and in the injured area. While wounds counted on fish caught during the summer months almost definitely reflect contemporary lamprey attack frequencies, scars represent attacks which occurred at an unknown previous time. The healing rate appears to be variable, so a scar cannot necessarily be attributed to current year lamprey activities. More important, well-healed scars which have lost the original wound shape and size can be confused with injuries of other origin, and this is a source of error in the data to be discussed, whose magnitude cannot be assessed.

It has been a convention among Canadian workers over the years, to describe lamprey attack frequency in terms of wounds counted per 100 fish. In the present offering both wounds per 100 fish and wounded fish per 100 sampled appear among the statistics, because the relationship between them provides a measure of the frequency of fish-bearing multiple wounds.

General Biology

HISTORICAL

As noted earlier, what sets the Lake Ontario sea lamprey apart from its upper Great Lakes descendents is that, like its counterpart stocks in the Finger Lakes of New York State (Gage 1928), it evidently coexisted for a long time with its prey. The question of whether the sea lamprey has lived in the lake since early postglacial times or has colonized more recently, as suggested by Aron and Smith (1971), is important, but it will not be addressed here. For present purposes the main question is why was there so little evidence of lamprey impact in earlier times? The pertinent facts are

1) The 1835 description of a lamprey from Duffins Creek, east of Toronto, by Fothergill, which was reported by Lark (1973) has been generally accepted as referable to *Petromyzon marinus* and this indicates that the sea lamprey has been a member of the Lake Ontario fish community for at least 145 yr.

2) There is a significant body of information about the fishery problems of Lake Ontario in the last century in reports and proceedings of hearings, but the lamprey was never identified as a significant threat to the premium fish stocks — in fact, it was scarcely mentioned

(Smith 1970; Christie 1972). The first observations of fish mortality caused by sea lamprey appear to have been those of C. W. Nash in the 1890s, as reported by Dymond et al. (1929).

3) The latter authors noted up to 14 lamprey marks on individual lake trout in the 1920s, but thought the lesions were largely superficial. They recognized the lamprey as a likely source of natural mortality among larger fish, but expressed no real alarm. They noted that lamprey were found attached to lake trout (*Salvelinus namaycush*) and were also known to prey on whitefish, burbot (*Lota lota*), ciscoes (*Coregonus* sp.), and longnose suckers (*Catostomus catostomus*) in the 1920s (Dymond et al. 1929).

4) Christie (1963) noted that "wounds and scars are commonly seen" on adult whitefish and presented a strong regression (Christie 1974, Fig. 4) between instantaneous total mortality levels and sea lamprey wound incidence on planted lake trout.

Two scenarios were offered in explanation for this historical sequence (Christie 1972). First it was suggested that the damming of Lake Ontario's tributaries which began early in the last century could have reduced production of parasitic sea lamprey, while the reopening of at least some of the rivers during this century could have had the reverse effect. The second postulation was that when the target species were present as abundant stocks of large animals, the lampreys behaved as parasites and did little damage. With intensified fishing and other human impacts which made the trout scarcer and individually smaller, the lamprey assumed a predatory role. The Nash observations around the turn of the century are consistent with this because there were significant numerical declines in both whitefish and lake trout stocks at that time (Christie 1963). Lett et al. (1975) examined this postulation in a mathematical model and offered further evidence of its viability. The two ideas are obviously not mutually exclusive.

The declines of the lake trout and burbot stocks from the 1920s toward their virtual extinction by around 1950 put more pressure on the single remaining important target species, the lake whitefish. While the collapse of the whitefish during the 1960s was no doubt speeded by eutrophication in the Bay of Quinte, the main spawning and nursery area (Hurley and Christie 1977), it was felt (Christie and Regier 1973) that adult mortality induced by the combination of lamprey predation and fishing pressure was excessive.

It is of special interest that the collapse of the burbot, lake trout, lake herring (*Coregonus artedii*), and whitefish stocks occurred in the western end of Lake Ontario many years before the eastern end (Christie 1972). in the years discussed here, therefore, and until salmonid plantings were begun recently, the deeper waters of western Lake Ontario were only inhabited by the small-sized alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) which are not known to be much utilized by the lamprey. The high summer wounding levels observed on white suckers (*Catostomus commersoni*) (Table 1) came mainly from western basin samples and this suggests that the suckers may have been the alternate host that allowed the sea lamprey to persist in that part of the lake. In the central basin, rainbow trout (*Salmo gairdneri*) and round whitefish (*Prosopium cylindraceum*) may have played similar roles. The collapse of both sucker and whitefish stocks during the 1950s and 1960s probably created a food shortage in the east where there were many observations of sea lamprey attached to carp (*Cyprinus carpio*) and walleye (*Stizostedion vitreum vitreum*) in the warm nearshore waters during the summer.

The most recent chapter of the Lake Ontario sea lamprey story began in 1971 with the initiation of control measures in the tributary streams. In the few years prior, however, coho and chinook salmon stockings were increased and the recoveries provide some measure of the effect of control. Wounding rates on adult spawning run salmon declined significantly through the 1970s as sea lamprey control and salmonid stocking reduced the lamprey:salmonid ratio. Figure 1 shows significant improvements in the size of stocked coho salmon returning to the Credit River (Fig. 3) coincident with the decline in wounding rates.

PREDATION PATTERNS

That sea lamprey inhabit the deeper waters of lakes in summer is widely accepted and Table 1 supports this. In the spring and fall, lamprey were found near the shore preying on white bass (*Morone chrysops*), carp, walleye, and northern pike (*Esox lucius*) among other species. The fisheries themselves tended to move offshore, and away from these stocks in summer, but the increasing predation on whitefish with the progress of the summer, and observations based on nearshore sampling (Hurley and Christie 1977) circumstantially suggested prey transfer.

Generally, lamprey did not attack smaller species nor those fish with heavy scales. When carp were attacked, the wounds typically appeared in the axils of pectoral fins where scales were smaller. As noted above, both seasonal predation patterns and prey selection were changed as the species composition changed.

In addition to the species already mentioned and those in Table 1, a complete list of Lake Ontario fish species known to be attacked by sea lamprey would include lake sturgeon (*Acipenser fulvescens*), chinook salmon, splake (*Salvelinus namaycush* × *S. fontinalis*), rock bass (*Ambloplites rupestris*), brown bullhead (*Ictalurus nebulosus*), gizzard shad (*Dorosoma cepedianum*), and large rainbow smelt.

Although lake trout were not abundant during the 1950 and 1960 decades, they were typically heavily wounded, whenever sampled. When the first introductions of coho salmon were made in the late 1960s predation by lamprey on the adults in late summer was extreme. Counts of four and five fresh wounds per

TABLE 1. Seasonal distribution of sea lamprey wounds on various fish species observed by Lake Ontario fishermen, 1954–63.

	Lake trout		Lake whitefish		Lake herring		White bass		White sucker	
	No. fish examined	Wounds/ 100 fish	No. fish examined	Wounds/ 100 fish	No. fish examined	Wounds/ 100 fish	No. fish examined	Wounds/ 100 fish	No. fish examined	Wounds/ 100 fish
Apr.	83	10.84	5 892	0.39	29	3.45	450	3.33	947	3.91
May	68	0.00	3 042	1.91	7	0.00	498	7.83	904	1.11
June	70	32.86	2 413	1.08	5	0.00	367	3.00	1000	1.60
July	72	43.06	4 613	6.57	14	7.14	82	0.00	206	3.88
Aug.	59	79.66	5 067	13.22	11	18.18	15	0.00	199	5.53
Sept.	12	175.00	3 785	4.97	544	0.00	85	3.53	404	2.48
Oct.	6	33.33	1 738	3.80	640	1.41	121	2.48	155	9.03
Nov.	4	0.00	3 787	4.12	1033	0.00	67	7.46	413	3.39
Dec.	—	—	793	1.01	—	—	—	—	—	—
Total	374	35.56	31 130	3.95	2283	0.57	1685	4.51	4178	2.87

	Blue pike		Walleye		Northern pike		Carp		Channel catfish	
	No. fish examined	Wounds/ 100 fish	No. fish examined	Wounds/ 100 fish	No. fish examined	Wounds/ 100 fish	No. fish examined	Wounds/ 100 fish	No. fish examined	Wounds/ 100 fish
Apr.	100	4.00	59	1.69	107	0.93	92	2.17	500	0.20
May	158	2.53	78	1.28	27	3.70	256	0.78	45	0.00
June	—	—	33	3.03	26	11.54	30	10.00	14	7.14
July	—	—	1	100.00	—	—	4	0.00	27	0.00
Aug.	—	—	27	0.00	—	—	30	0.00	27	0.00
Sept.	—	—	83	0.00	3	0.00	17	11.76	32	6.25
Oct.	6	0.00	246	2.44	65	20.00	41	7.32	283	3.18
Nov.	20	0.00	279	1.08	199	4.02	139	2.88	30	3.33
Dec.	—	—	45	2.22	—	—	—	—	—	—
Total	284	2.82	851	1.65	427	6.09	609	2.63	958	1.46

fish were not uncommon, but more significantly, the counts were quite inexact because a single lesion frequently consisted of a track of destroyed epithelium up to 203 mm in length, and these wounds crisscrossed the fish and complexed. The judgment at that time was that many of these severely attacked fish could not have survived because of the extent of the integument loss alone.

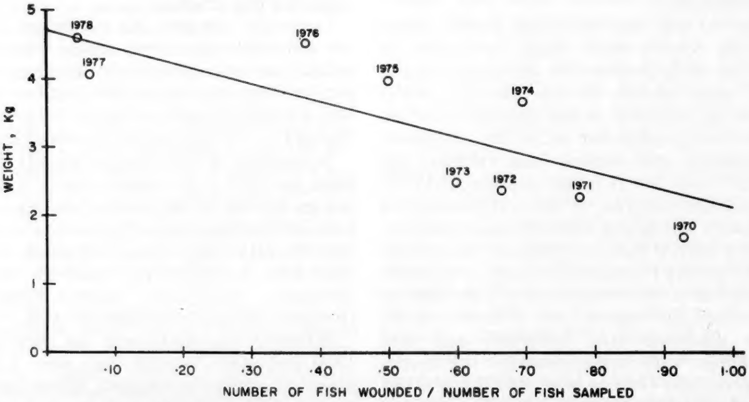


FIG. 1. Relationship between incidence of wounding and average weight of adult coho salmon returning to the Credit River, 1970–78 ($r = -0.814$).

LAMPREY GROWTH

Applegate (1950) suggested that ammocoetes metamorphose and descend from the streams in the fall or spring and live in the lakes for 18 mo or less. Dymond et al. (1929), however, examined a sample of 64 feeding adults from western Lake Ontario in 1928 and inferred from the size frequency distribution that the species might spend two or possibly three summers in the lake.

The lengths of lamprey collected at the same time in different years (Fig. 2) was fairly consistent but it is noteworthy that the standard deviations around the monthly means increased steadily from May onwards. That the animals collected early in the summer were uniformly small suggests a simple life history involving only a single summer spent feeding in the lake. It is taken that the large variance increase in fall is consistent with the Beamish and Potter (1972) observation of fall transformation at Shelter Valley Creek, but it does not rule out spring descent.

A further point should be noted in connection with Fig. 2. The largest sea lamprey seen by Dymond et al. (1929) was 470 mm in length and the record for our collections was 591 mm. It can be taken, therefore, that there is little if any recruitment of the large anadromous sea lampreys from the St. Lawrence River during the open water feeding period. This does not, of course, eliminate the possibility of immigration at an earlier life history stage because Beamish (1980) has shown that newly metamorphosed adults of anadromous populations are not larger than the freshwater forms and that the adults are only larger by reason of advanced age.

SOURCES OF PARASITIC PHASE SEA LAMPREY

There are few known sea lamprey spawning streams in the western section of the U.S. shore (Fig. 3). As Greeley (1939) pointed out, these tend to be low-gradient, warmwater streams, and likely unsuitable for lamprey reproduction on that account. In the northeast, streams tributary to the Bay of Quinte support sea lamprey, but from there eastward to at least Gananoque in the St. Lawrence River, the tributaries

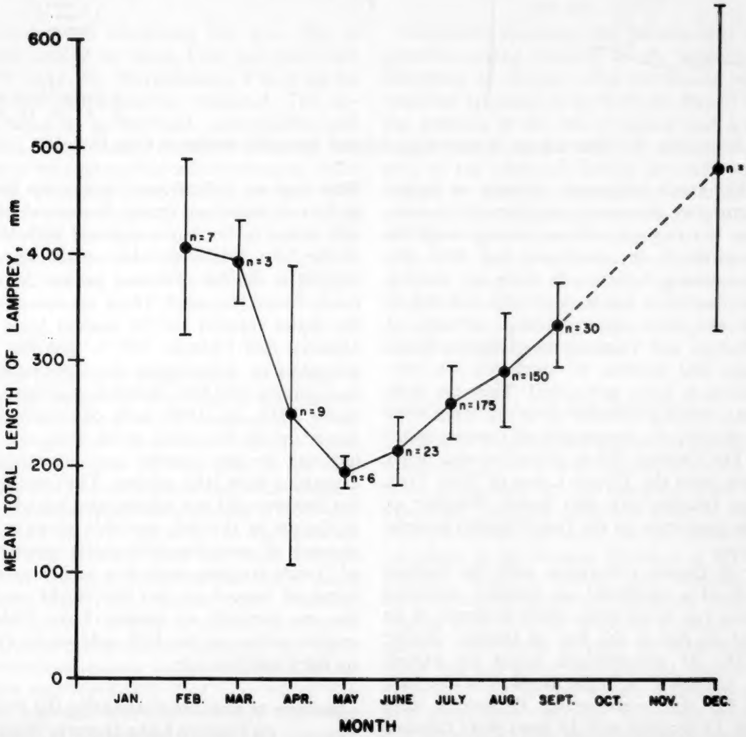
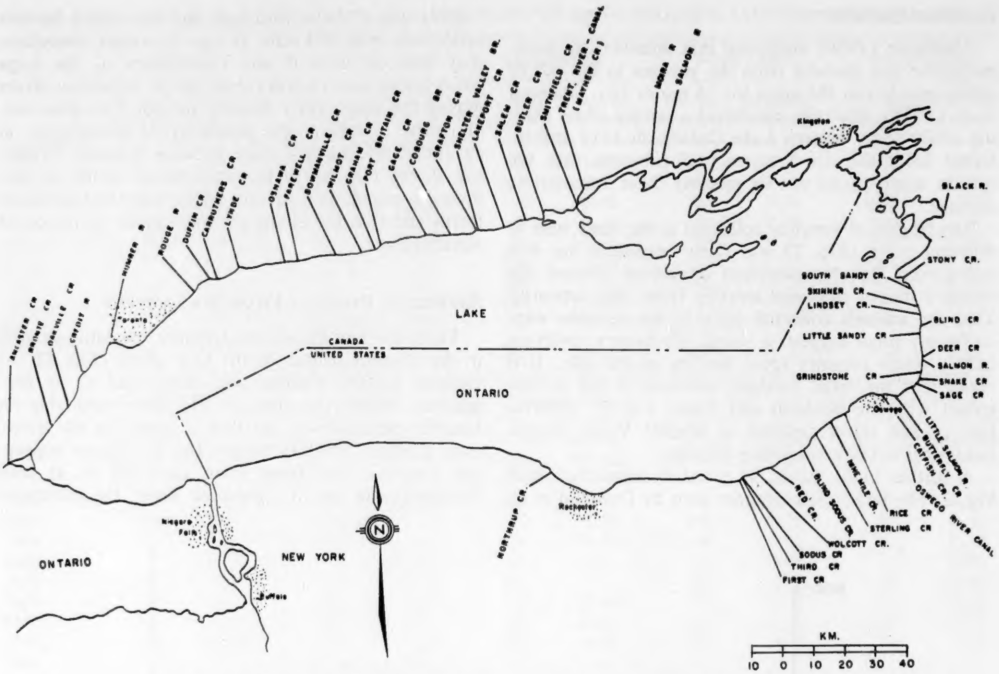


FIG. 2. Growth of parasitic phase sea lamprey in eastern Lake Ontario (1954–64); means and one standard deviation shown for each month.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PORT BRITAIN CR
GAGE CR
COBOURG BR
GRAFTON CR
SHELTER VALLEY BR.
LAKEPORT CR
SALEM CR
BUTLER CR
SMITHFIELD CR
TRENT, RIVER - CANAL (MAYHEW CR)
MOIRA R
SALMON R
Kingston
BLACK R.
STONY CR.
SOUTH SANDY CR.
SKINNER CR
LINDSEY CR.
BLIND CR
LITTLE SANDY CR
DEER CR
SALMON R.
GRINDSTONE CR
SNAKE CR
SAGE CR
Oswego
LITTLE SALMON R.
BUTTERFLY CR
CATFISH CR.
OSWEGO RIVER CANAL
NINE MILE CR.
RICE CR
STERLING CR
BLIND SODUS CR.
RED CR.
WOLCOTT CR.
SODUS CR
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FIG. 3. Distribution of known sea lamprey spawning streams in Lake Ontario.

tend to be either small temporary streams or larger streams with natural or man-made impediments to lamprey migrations. For the rest, streams issuing from the Adirondack foothills in the southeast and from the drumlins and moraines of the north shore are suitable and used where they have not been grossly polluted or blocked. There are three major drainage systems of interest. The Rideau and Trent rivers of the northeast both drain large lake systems to which the sea lamprey is not known to have penetrated. They are both blocked by locks, but it is possible these are made even more effective obstacles by reason of high summer water temperatures. The Oswego River system carries water to Lake Ontario from the Finger Lakes of New York State where sea lamprey are also found. Whether or not these stocks contribute to the Lake Ontario populations is not known.

Of the Bay of Quinte tributaries, only the Salmon River is considered a significant sea lamprey spawning stream, but there has never been much evidence of its parasitic output on fish in the Bay of Quinte. During 21 yr (1958–78) of observations based on experimental gillnet catches at a single location in the bay, a total of 78 303 fish representing 37 species were examined. Only 13 wounds and 19 scars were counted on 17 410 fish in nine of the larger species. The netting was generally conducted between May and October, but in the 3 yr when it ran through the full 12 mo, there was no indication of heavy sea lamprey activity in the fall, winter, or spring. In general, attack incidence was trivial in the bay compared with the open waters of the lake. Whitefish taken in the Bay of Quinte for tagging in the fall spawning period, for example, were rarely found wounded. These spawning runs constituted the major support for the eastern basin gillnet fishery (Hurley and Christie 1977), and the very common wounding by sea lamprey there will be illustrated later. In a sample of 1536 whitefish examined in the bay between 1955 and 1960, only one fresh wound was observed, while the count of 86 scars was more in keeping with the late summer scarring frequencies for fish examined from lake catches. The conclusion is that the sea lamprey did not accompany whitefish into the Bay of Quinte in the fall, and this, along with the general absence of predation indicators, suggests that the Bay of Quinte lamprey spawning runs were unimportant in terms of impact on the fish stocks, and further, that the sea lamprey of eastern Lake Ontario had their origins either on the U.S. side or further to the west on the Canadian side.

Sources of Error in Estimating the Predation Rate on Eastern Lake Ontario Whitefish

VARIATIONS WITH WHITEFISH SIZE AND AGE

Figure 4 shows that wound frequency tends to in-

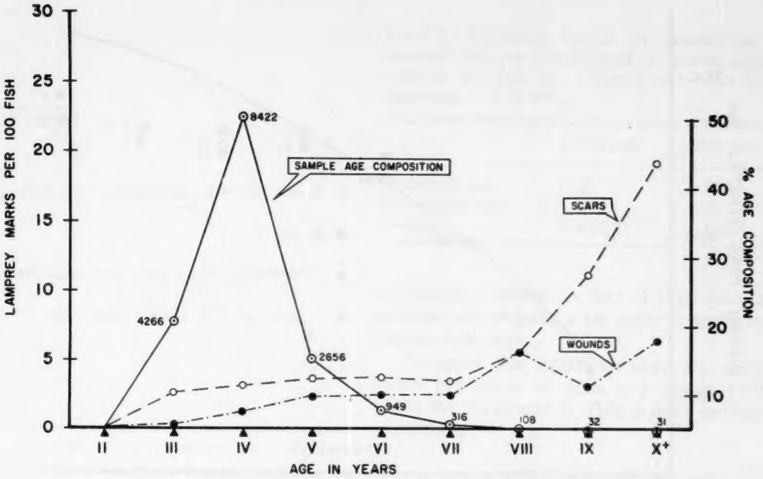

FIG. 4. Sea lamprey wound and scar frequencies in relation to the summer age and size distribution of whitefish (1954–61). Included numbers represent sample size.

crease only slightly with advancing fish age. This is because fish size tended to show little increase over the ages IV–VII (Fig. 5). Nevertheless, Fig. 6 shows that larger fish are more heavily wounded. The accumulation of scars is, by contrast, age-specific, and Fig. 4 shows that the extremely small numbers of fish which survived to be captured at advanced ages, were nearly all scarred. The steeply exponential increase with age probably indicates improved survivorship among fish wounded beyond the age of VII. Note that this contention is supported by the improvement in annual growth increment between ages VI and VII, in Fig. 5.

SEASONAL VARIATIONS

Wounding also varies seasonally (Fig. 7). Table 1 showed that during the period of whitefish dominance, fish with typically nearshore distribution tended to be attacked in spring and fall. There is no evidence, however, of significant predation on whitefish in the fall, winter, or spring at the east end of the lake. During 2 yr of winter commercial catch sampling (1957 and 1958), examination of 1381 whitefish in the October through April period revealed only one fresh wound, while during May through September of those years 110 fresh wounds were found among 3851 whitefish (3%). As noted earlier, lamprey have not been found in the Bay of Quinte in significant numbers, and since the above observations mainly concern Lake Ontario catches (October and November data were mixed bay and lake catch samples), it is reasonable to infer that this is further support for the contention that lamprey found in the eastern basin of Lake Ontario are produced in streams outside it.

Generally speaking, the picture was one of a progressive coming together of the lamprey and its prey, climaxing in August. The movement of most of the whitefish appeared to be from the Bay of Quinte spawning grounds in the fall or spring and a return toward deeper water as the summer advanced. Most of the area of the whitefish fishing grounds was between 27 and 55 m with the average closer to 27. Since catch-per-unit-effort usually peaked in July, it is inferred that the fish reached their feeding grounds before the lamprey. The fish became less available to nets, and apparently lamprey as well, by later September, and it is believed these movements were associated with, or presaged the spawning migrations to the Bay of Quinte which took place in October.

EFFECT OF GILLNET SET DURATION

Various observations led to the belief that whitefish which had already been enmeshed in the gill nets were more vulnerable to the lamprey. This represented a significant potential source of error in estimating lamprey predation incidence on the whitefish because of variations in the average duration of net sets. First, set duration declined through any summer season while lamprey wound frequency increased from June through August (Fig. 7) and seasonal averages of wound frequency were likely in error to some extent when this effect was not taken into account. Secondly, and more important, the decline of the whitefish stock resulted in a progressive decrease in annual average set duration with time. This likely happened because fishermen invested increasing time in the capture of other species as the whitefish decline progressed, and gillnet sets for

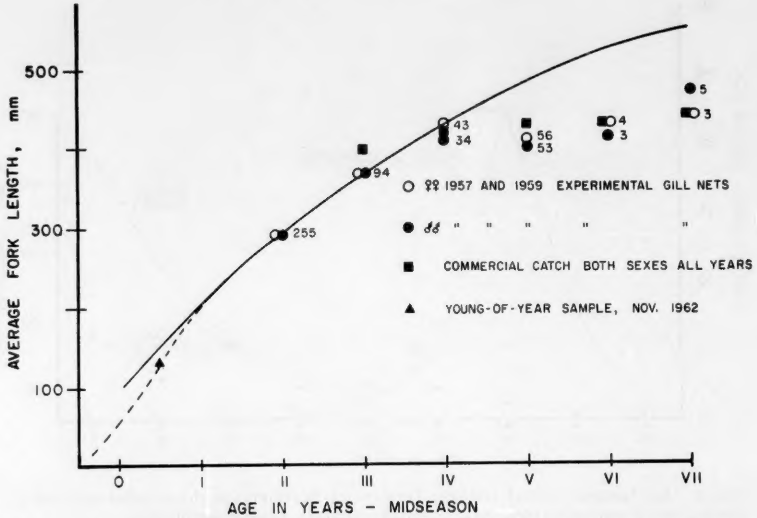

FIG. 5. Size for age relationship in Lake Ontario whitefish. Solid line based on a Walford graph derived from experimental gillnet catches of 2- and 3-yr-old fish with L∞ fixed at 711-mm fork length.

whitefish became trial efforts with both lower frequency and duration. There was a danger therefore that the impact of the lamprey, as measured by the incidence of wounds, appeared relatively less important in the final years of the fishery.

The best evidence that duration of gillnet set influenced the lamprey wound frequency is found in the incidence of multiple wounds. Multiple wounds were observed relatively infrequently on the whitefish, but their appearance was related to both fish size and set duration. Data from one-night sets, or durations exceeding three nights were atypical for the summer period and disregarded on this account. The catches examined in the 1954–63 period were classified accord-

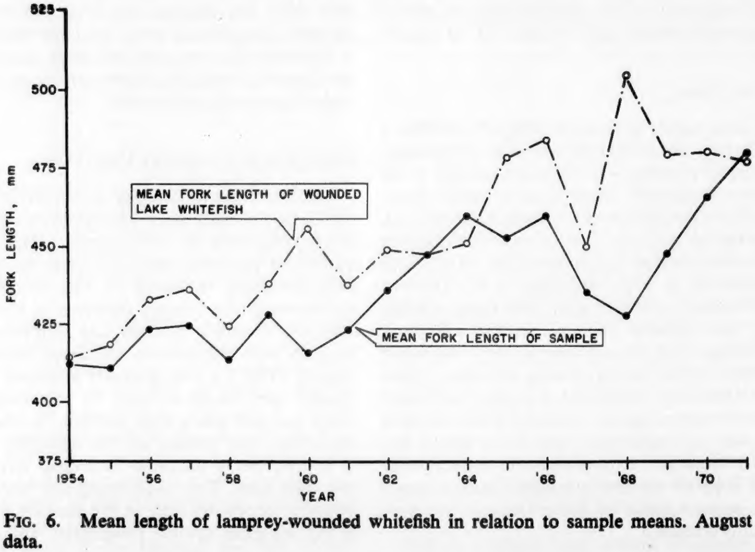

FIG. 6. Mean length of lamprey-wounded whitefish in relation to sample means. August data.

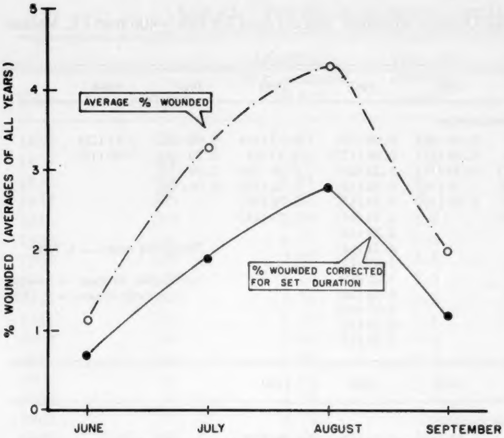

FIG. 7. Seasonal pattern of lamprey wound frequency on whitefish (1954–68).

ing to set duration, the fish examined in them by size, and the regression slopes for multiple wounds were calculated (Table 2). The slopes were higher both for larger fish, and for catches examined from sets of longer duration, indicating that the expectation of multiple wounds was higher in both cases. This illustrates two important effects. First, it can be inferred that among whitefish already enmeshed in the nets, lamprey select for the larger fish. Secondly, even within a size-class, longer set durations increase the probability of multiple wounding and it is taken that the relative immobilization of whitefish in the gill nets makes them more attractive or easily attacked prey for the sea lamprey.

RANDOM ERROR

The foregoing suggests that longer set duration can cause significant overestimation of relative lamprey abundance between seasons and between years. The first obstacle to correcting for this effect, however, lies with the large inherent variance in lamprey wound frequency between catches. The data in Table 3 have been segregated from the whole archive to account for season, fish size, year, and set duration, and it will be observed that the means for the samples in any year are not normally distributed. The arrays are, however, significantly different from the Poisson distribution and this is evidence that there is a patchiness to the occurrence of lamprey wounds on whitefish in time and/or space. On this basis it was concluded that arithmetic averages were inappropriate for development of the corrections for variations in set duration.

TABLE 2. Regression slopes for wounds per 100 fish on wounded fish per 100 sampled in catches segregated by set duration and fish size. (*Significant — $P > 95\%$; **Highly significant — $P > 99\%$.)

	≤404 mm	≥406 mm	*t* values
Two-night sets	1.02	1.17	3.1896**
Three-night sets	1.09	1.26	2.1301*
t values	3.4107**	2.1456*	

The data sets in Table 3 were therefore fitted to the negative binomial distribution and then transformed. This model was chosen strictly as an empirical tool, in full recognition that understanding the distribution of lamprey relative to that of their prey at any point in time will demand a far more sophisticated sampling design than ours.

To apply this model we used the maximum likelihood procedure of Bliss and Fisher (1953) to estimate the parameter *k*. This is done iteratively with the equation:

$$(1)\quad N \ln (1 + \bar{x}/\hat{k}) - \sum^{J}(Aj/(\hat{k} + j)) = 0$$

where N is the sum of the frequencies, A's are frequencies for wound class intervals J, accumulated from the right-hand tail of the distribution, and $\bar{x}$ is the mean percentage of wounds per sample. The k values were used to transform the sample percentages (x) in the expression:

$$(2)\quad x = \ln (x + \tfrac{1}{2}k).$$

All the negative binomial fittings were satisfactory in χ^2 terms. The k values established were 0.3873 for the two-night data and 0.7543 for the three-night data. The results of the procedure are outlined in Table 4. This was an interesting result because, since small values of k represent higher degrees of contagion, it may be that while the probability of attack in the wild is subject to variability controlled by the schooling of the whitefish or the patchiness of lamprey, or both, the attacks on fish already enmeshed is more random.

The Kolmogorov–Smirnov Two-Sample Test (Siegel 1956) was applied in the right column of Table 4 to measure the significance of the mean differences. Chi^2 for the mean difference between the adjusted arithmetic arrays approaches but does not achieve significance, and this illustrates that, while this particular transformation appears to be useful for adjusting variance in lamprey wounding data for statistical purposes, the limited number of samples available made this a less robust test of the set duration effect than that outlined in Table 2. The level of difference between the two set durations examined (18.2%) is substantial, however, and it is the best estimate these data can provide.

POSSIBLE BIAS DUE TO DEATH OF ENMESHED FISH

Another potential source of error lay with fish which died in the gill nets. These fish were dressed immediately after capture and because they were prone to rapid spoilage, fishermen did not like having them

TABLE 3. Lamprey wound frequencies in sampled catches of Lake Ontario whitefish. August data for fish ≥406 mm FL. Values are percentages, with sample numbers in parentheses.

1954	1955	1956	1957	1958	1960	1961	1962	1963	1964	1969	
					Two-night set duration						
25.64 (39)	0.00 (51)	5.36 (56)	6.06 (33)	0.00 (28)	0.00 (6)	0.00 (49)	0.00 (50)	4.17 (48)	0.00 (31)	2.63 (28)	
4.88 (41)	0.00 (27)	0.00 (27)	26.39 (31)	3.23 (31)	0.00 (6)	0.00 (75)	0.00 (122)	16.67 (6)	4.76 (21)	0.00 (14)	
4.08 (49)	6.25 (64)	3.45 (58)	0.00 (35)	8.24 (85)	5.88 (17)	4.23 (71)	1.28 (84)	0.00 (31)	2.94 (34)		
	3.51 (57)	7.69 (78)	0.00 (26)		3.16 (34)	1.79 (56)	0.00 (18)	0.00 (20)	0.00 (48)		
	4.65 (86)		0.00 (15)		0.00 (17)	0.00 (48)	6.25 (32)	7.78 (90)			
	5.71 (35)		8.00 (25)		0.00 (10)		2.44 (41)	2.27 (44)			
	16.67 (18)		3.57 (28)				2.27 (44)				
	3.42 (59)		4.11 (25)				6.25 (16)				Weighted mean = 3.73%
	0.00 (13)		0.00 (14)				5.88 (17)				
	3.80 (27)		12.50 (16)				7.41 (27)				Arithmetic average of annual arithmetic means = 3.79%
	0.00 (18)						0.00 (28)				
	4.35 (23)						2.11 (96)				
							0.00 (39)				
							0.00 (24)				

1954	1955	1956	1958	1959	1960	1961	1962	1963	
					Three-night set duration				
7.69 (39)	10.67 (75)	7.41 (135)	0.00 (17)	1.28 (78)	5.56 (18)	4.08 (49)	1.75 (57)	4.00 (25)	
13.04 (23)	7.89 (38)	2.33 (43)	5.00 (20)	2.99 (36)	11.11 (9)	0.00 (35)	6.67 (15)	3.26 (92)	Weighted mean = 5.19%
12.00 (100)	7.09 (43)			2.13 (47)	17.65 (34)	0.00 (30)	0.00 (18)	0.00 (23)	
9.09 (22)	0.00 (20)					0.00 (20)	0.00 (25)	6.45 (31)	Arithmetic average of annual arithmetic means = 5.01%
	14.29 (7)						0.00 (21)	0.00 (2)	
	10.00 (40)						1.85 (61)		

handled in the sampling process. The numbers of such fish sometimes became quite high in late summer (to one-half or more of the whole catch in extreme cases), and they increased sharply with duration of set. The concern was that those portions of the catches not examined might have contained higher percentages of wounded fish, thus biasing the wounding frequencies. The data showed, however, that wounding rates in the samples were uncorrelated with the frequency of dressed fish in the catches, for any size-classes or set durations. Further, it was impossible to establish that dressed fish contributed significantly to the variance from regressions of wounded fish on sample. The conclusion was, therefore, that the fish which died in the

TABLE 4. Variance in lamprey wound statistics for Lake Ontario whitefish. August data for fish ≥406 mm FL. (*$\chi_{05}^2 = 11.07$, df = 5; **$\chi_{05}^2 = 5.99$, df = 2; ***derived and used to correct the next row.)

	Catches from two-night set duration				Catches from three-night set duration				Kolmogorov–Smirnov** 1 tail-2 sample χ^2
	$\bar{x}$	SD	χ^2	k	$\bar{x}$	SD	χ^{2*}	k	
1. % wounded values uncorrected for between-years variance	3.79	5.35			5.01	4.88			
2. % wounded corrected for between-years variance	3.92	4.57	4.61	0.4366***	5.02	4.93	12.44	0.7548	2.47
3. 1st correction by negative binomial means	3.44	4.24	6.81	0.3992	4.29	4.61	5.63	0.7329	
4. 2nd correction by negative binomial means	3.41	4.33	4.85	0.3720	4.10	4.46	4.03	0.7543	
5. 3rd correction by negative binomial means	3.44	4.28	4.02	0.3873	4.09	4.41	4.03	0.7543	5.13
6. 4th correction by negative binomial means	3.46	4.25	5.06	0.4070					
7. Negative binomial transformations for row 6 (two nights) and row 5 (three nights)	0.351	1.592			1.06	1.01			14.20

TABLE 5. Statistics of sea lamprey predation on Lake Ontario whitefish. August data.

						Average fork length (mm)	
Year	Sample	Observed avg. wounds /100 fish	Avg. set duration nights	% wounding corrected to 0 nights[a]	% increase per night of set duration	Sample (FL_s)[b]	Wounded (FL_n)
1954	572	10.97	2.8	6.14	1.75	411	414
1955	1286	6.38	2.3	3.85	1.10	411	419
1956	581	3.91	2.7	2.21	0.63	424	432
1957	555	6.08	2.1	3.80	1.09	424	437
1958	294	2.59	2.4	1.54	0.44	414	424
1959	256	4.35	2.4	2.58	0.74	429	439
1960	353	2.96	2.6	1.70	0.48	417	457
1961	877	1.14	2.5	0.66	0.19	424	437
1962	156	2.36	2.5	1.38	0.39	437	450
1963	215	5.36	1.9	3.47	1.00	447	447
1964	351	0.84	1.6	0.58	0.16	460	452
1965	323	4.09	1.2	3.04	0.88	452	478
1966	61	4.62	1.4	3.30	0.94	460	485
1967	73	5.39	1.3	3.93	1.12	434	450
1968	219	0.74	1.2	0.55	0.16	429	505
1969	166	6.26	1.0	4.87	1.39	447	480
1970	426	8.55	1.0	6.65	1.90	465	480
1971	93	1.39	1.0	1.08	0.31	480	478

[a] Observed wounding plotted on set duration and line carried to ordinate to satisfy:

$$\frac{\%\ \text{increase/night (slope)}}{\%\ \text{at 0 nights (intercept)}} = 0.286 \text{ (see text)}$$

[b] $FL_n = 80.68 + 0.853\ FL_s$

$r = 0.68$.

nets were probably more or less randomly distributed across fish sizes, and their frequency did not likely affect lamprey wounding frequency in the samples.

ADJUSTMENTS TO THE DATA SERIES

For the long-term averages the proportion of wounded fish in nets set for two nights was 3.46 and this advanced to 4.09 for samples examined from nets set for three nights, and we infer that nets set for one night at these levels of lamprey density would have yielded 2.83 (i.e. 3.46–0.63 wounds per 100 fish), and the wound frequency outside of the nets would have been 2.2 wounds per 100 fish. It would have been useful to have a broader range of set durations to test the assumption of linearity, but the model does apply where new fish enter the nets at a constant rate on each night of the duration of the net set, and the prob-

TABLE 6. Population statistics for Lake Ontario whitefish and lamprey.

Year	No. age IV+ whitefish caught (1000s)	Exploitation rate	Spring population age IV+ (100s)	Aug. corrected wound frequency wounds/100 fish	Lamprey density index (column 4 × column 5)
1954	63.8	0.399	1600	6.14	9 824
1955	116.8	0.464	2520	3.85	9 702
1956	292.0	0.581	5030	2.21	11 116
1957	102.7	0.649	1580	3.80	6 004
1958	63.8	0.658	970	1.54	1 494
1959	148.2	0.701	2110	2.58	5 444
1960	66.6	0.784	850	1.70	1 445
1961	261.8	0.613	4270	0.66	2 818
1962	145.3	0.585	2480	1.38	3 422
1963	129.5	0.633	2050	3.47	7 114
1964	38.5	0.433	890	0.58	516
1965	27.2	0.269	1010	3.04	3 070
1966	15.9	0.198	800	3.30	2 640
1967	10.1	0.295	340	3.93	1 336
1968	19.7	0.281	700	0.55	385

ability of a lamprey encountering an already enmeshed fish is constant and unaffected by the density of fish already in the nets. Both these assumptions are probably viable for the ranges of fish and lamprey densities encountered here. We assume that the rate at which wounds are accrued by enmeshed fish is proportional to the wound frequency on free fish. Thus:

(3) slope/intercept = 0.63/2.2 = 0.286 = a constant.

To find corrections for individual values we used a simple graphical procedure. When average wounds per 100 fish were plotted against average set duration in nights for any monthly or annual value, a line was fitted from the datum to the ordinate to satisfy the above relationship. The intercept and slope values thus derived for August data over all years appear in Table 5, and the intercept values are the "corrected" percent wounding data appearing in Table 6. Averages of the monthly values so corrected appear as the lower line in Fig. 7.

Figure 7 suggests that the corrections to seasonal trends in set duration were not sufficient to produce a significant difference in the within-season wound frequency pattern. This was not the case with the time series, however. Table 5 shows that the set duration values dropped from an average of about two and a half nights before 1962 to values approaching one night after the late 1960s. The wound frequency data in the third column of Table 5 show the reciprocal trend, and the same averages corrected to zero nights set duration (column 5) do not trend so steeply downwards. The overall trend is not eliminated by the correction, however, and this will be discussed in the next section.

Lamprey Abundance and Impact on Whitefish

The whitefish population estimates in Table 6 derive from the application of the Paloheimo (1961) linear formula as previously reported (Christie 1978). The present analysis has revealed that the mortality values are somewhat underestimated, perhaps as a result of the relative meshing efficiencies (size of the fish suggests a severely cacometric situation (Christie 1978)), and this in turn underestimated the catchability coefficient and the exploitation values in Table 6. This means that the population values are overestimated somewhat, and if the suggested reason is correct, the values for the last few years of the whitefish fishery may be somewhat underestimated because of reduction of fishing effort. This possible effect would be complicated, and possibly counteracted by relaxation of competition between gear units, and our view is that the estimates are probably internally consistent. That they may be close to realistic values is supported by the fact that a Petersen population estimate for 1955, the only year in which tag returns were not biased by nonreporting error, was very close to the value here. The unfortunate aspect is that no analysis of the partitioning of the mortality coefficients can be attempted within these data at present.

Table 6 brings together these population estimates with the August wound frequency data corrected for differences in set duration, to produce an index of sea lamprey density in eastern Lake Ontario. The statistic is presented primarily as a means of dissociating the wounding frequency from fish abundance. With the low overall frequency of wound incidence it is tempting to suggest that one wound observed in a single month of sampling represented the total efforts of a single lamprey, but this could be misleading. Some wounds represented attacks interrupted by the capture of the fish, and others represented attacks which had been completed prior to capture. We could not distinguish one type from the other. In either case the lamprey involved could have, and likely did attack again, but it seems very likely that a lamprey interrupted in midmeal would have begun hunting again sooner. We must consider the possibility therefore, that under more intensive fishing conditions, wound frequency could have been artificially increased. The general effect of repeated attacks by the same lamprey is to overestimate lamprey density, and the potentially more serious effect of the tendency of fishing activity to interrupt feeding is to create an exaggerated picture of the decline of the lamprey, as fishing pressure decreased in the 1960 decade. We have no way to evaluate the importance (if any) of the latter effect in these data, and can only proceed on the assumption that it was not a major factor.

With this precaution in mind, we note that the trend in lamprey density shown in Table 6 is toward reduced abundance after the first 3 yr of observation, and that between years differences were apparently as great as 11-fold. Even more interesting is the general paralleling of the whitefish and lamprey density values (Table 6). It is difficult to interpret a simultaneous lamprey and whitefish decline other than in terms of lamprey mortality which varied inversely with prey density in this simple predator–prey situation.

The most notable exceptions to the general correlation occurred in the years 1961 and 1962, and it might be inferred that the lamprey year-classes were not large enough to take advantage of the large 1957 year-class of whitefish which swelled the stock in those years. The total population of whitefish was larger in earlier years and lamprey density proportionally large also, so the low relative lamprey densities of those 2 yr may have resulted from poor year-classes. Otherwise, the impression is one of ample stream output of transformed animals to meet the available prey levels. The other departures from the general correlation occurred in the earliest years, 1954 and 1955, where lamprey density was high relative to whitefish density. One possible explanation is that the greater abundance of white suckers (their decline is known to have happened in the late 1950s) at the time provided additional support for the survival of a large lamprey population.

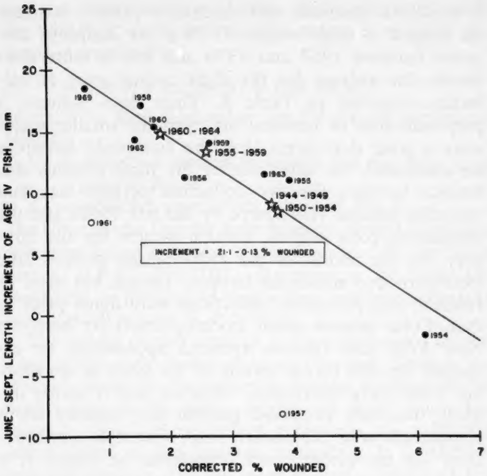

FIG. 8. Effect of lamprey predation on within-season growth of 4-yr-old Lake Ontario whitefish.

Returning to the more conventional consideration of effect of sea lamprey on the whitefish, the data offer an interesting paradox. On one hand there is evidence of heavy cropping rate by the fishery in Table 6, and on the other, evidence of a significant lamprey impact. The size-for-age data in Fig. 5 show the size-selective mortality effect reported originally in Christie (1963). Data from collections of prerecruit whitefish were used along with a long-term length maximum of 711 mm in a Walford graph (Ricker 1975) to construct a theoretical growth curve. The scallop between ages IV and VI reflects a lamprey rather than a fishery effect because the annual (June–September) length increments measured for age IV fish were uncorrelated with the exploitation rates ($r = +0.49$), but highly correlated with the lamprey-wounding indices (Fig. 8). In this figure, years where either or both of the months of June and September were not sampled, and two odd years, 1957 and 1961, were not included in the regression; the resulting correlation for the nine data pairs is very strong ($r = 0.94$). Taken with the evidence of Fig. 4 that few fish accumulate scars between age IV and V, this is suggestive that the sea lamprey can take a sufficient toll among the larger or faster-growing fish, to effectively freeze fish size. No similar relationship appeared among the older age-groups, but this is understandable in view of the size variation which was seen among those fish which survived the heavy age-IV mortality.

Figure 6 indicates that either because of selective mortality in small fish, or preference for larger fish by the lamprey, wounds are more often seen on larger fish. The data discussed earlier showed that multiple wounds were more frequently seen on the large fish, and this could mean that smaller fish are less likely to survive even one attack. Figure 8, however, allows no other interpretation than a selective removal of the larger whitefish by the lamprey. The reconciliation must be that multiple wound frequency was a simple function of wound incidence, and even though the young whitefish died quickly upon attack, relatively fewer of them were attacked by lamprey.

TABLE 7. Size relationships between sea lamprey and lake whitefish in Lake Ontario, 1954–64.

Month	Lamprey avg. weight, g	Whitefish avg. weight, g	Lamprey-whitefish weight ratio, %
May	7.7	986	0.8
June	11.3	1055	1.1
July	22.7	1092	2.1
Aug.	34.5	1065	3.2
Sept.	56.2	1046	5.4
Average	26.5	1049	2.5

The earlier observations (Fig. 7) on the seasonality of lamprey wound incidence on whitefish may not exactly parallel seasonal trends in mortality resulting from the attacks. This is so because the small lamprey seen early in the summer may have been less lethal in their effect (Table 7). The lamprey weight averages correspond to the monthly length averages shown in Fig. 2 as calculated from:

(4) $\log_{10} W = 3.627 \log_{10} L - 37.79$

where W = weight in g and L is length in mm.
The whitefish weight values given were those measured in the commercial catch samples, for fish of all ages.

The weight ratios (Table 7) show that lamprey size increased from less than 1 to more than 5% of the whitefish weight over the course of the predation period. As noted earlier the slow accumulation of scars up to age VII in Fig. 4 suggested a constant low survival of wounded fish. Beyond age VII, the rate of accumulation was much faster, and this corresponded with the reappearance of annual growth increments. Whitefish at age VII averaged 1257 g. This approximates the average at the end of July and the corresponding lamprey weight average from Table 7 would be 28.6 g. This yields a lamprey: whitefish weight ratio of 2.3% and this is the threshold value below which whitefish survival is significantly improved. We suggest therefore that Table 7 indicates that wounding measured before August inflicted less mortality on the whitefish, and because the wound frequencies fell in September, August was the main period of lamprey impact on the whitefish stock.

In the discussion of Fig. 2 the relatively narrow range of size variation in lamprey collected at the same time in different years, was noted. At this point it is useful to examine the variance in relation to the

TABLE 8. Analysis of Lake Ontario sea lamprey growth and the predator-prey statistics.[a]

Year	Avg. August weight, g	Length C of V %	Inst. weight gain July–August[b]
1954	36.0	9.7	2.56
1956	37.6	11.1	2.70
1957	50.9	11.5	3.30
1960	38.6	1.9 (3)	2.97
1961	30.3	14.9	2.08
1962	26.1	11.1	2.17
1963	24.9	16.1	2.50
1964	39.1	13.0	2.77
Average	32.2		2.63

Correlation coefficients

August weight average on August wounding % — 0.19
August weight on lamprey density index — 0.03
Instantaneous growth on August wounding % — 0.27
Instantaneous growth on lamprey density — 0.05
Length variance on August wounding — 0.05
Length variance on lamprey density — 0.17

[a] See Table 6.
[b] Log_e (August weight–July weight).

abundance statistics of Table 6. Table 8 gives the August average weights (converted from length data which were more often taken, by equation (4)) for the lamprey collections. Only July and August were consistently included in the 8 yr of collection, and so the growth rate (instantaneous) was calculated for these data only.

The correlation coefficients which appear in Table 8 are all statistically nonsignificant. There is an obvious danger in placing too much confidence in eight data points based on small sample averages, but it is important to note that the predator–prey ratios varied 11-fold while the lamprey size averages only varied by a factor of 2 and the growth rates varied 1.6-fold. This implies that large-sized lamprey, or fast lamprey growth appeared to have equal likelihood of occurrence in years when lamprey were dense relative to their prey, as in years when low relative lamprey density might have been expected to produce better lamprey growth.

The first point of interest here is that if lamprey mortality is determined by prey density, smaller lamprey likely die first, and the lamprey might have maintained a fairly constant average size as a result. This suggests that lamprey which survive become larger and where prey density is high, lamprey survival improves to the point where food supply limits ultimate size. This is obviously highly speculative but for the present, it appears to be the best explanation. The concept invites more detailed studies of lamprey survival and growth.

The second point is that lamprey growth may to some extent be a function of the kind of prey which is available. Johnson and Anderson (1980) indicate an August average weight of 71 g for lampreys collected between 1967 and 1976 and this is more than double the average for the eight earlier years of collection reported in Table 8. Their data indicate a preponderance of females, but even the smaller males were a great deal larger than the (unsexed) lampreys we examined. As noted earlier the most obvious difference between the two collection periods was that whitefish became very scarce by the late 1960s and the introduced coho salmon became targets for the lamprey. By the middle of the 1970 decade stocked lake trout provided additional lamprey forage, but most of Johnson and Anderson collections were made prior to that. Coho salmon smolt stocking levels by both the New York and Ontario agencies approached or exceeded 500 000 fish in several of the years in question, but these were distributed lakewide and it seems unlikely that they produced general prey density levels comparable with the eastern basin whitefish concentrations (of the earlier years considered, at least). It is our view therefore, that the lamprey growth response was more likely related to the presence of large salmonids, than to their density.

The theoretical whitefish growth curve of Fig. 5 suggests that the growth increment between age IV and age V should be about 23 mm. Figure 8 has its intercept for growth increment of age IV fish in the absence of lamprey at 21.1 mm. Given that the June–September period probably does not cover the entire growing season, this can be considered good agreement.

The points marked with stars in Fig. 8 are 5-yr averages. For the 1955–59 and 1960–64 periods they represent observed average increments and wounding averages. The 1944–49 and 1950–54 points represent averages for the increments only and they were placed on the line of fit. Given the position of the 1954 value, the inference is that lamprey wound incidence may have only been very high in the 1954–55 period. The placing of the 1944–49 point would suggest possibly heavy wound incidence levels during that period. If so, lamprey population levels of that period were high relative to significant residual levels of burbot, lake trout, white sucker, and a considerably larger whitefish population (Christie 1963). This may have been the case, but it is at least equally likely that the 1944–49 whitefish growth increments were smaller because of the greater whitefish stock density levels. The plotted average lengths for all ages in that period show the age IV–VI scallop, but it is shallower than that indicated for the 1950–54 averages. This suggests that size-selective lamprey mortality and density-dependent growth were probably both involved. The age IV mean length value for the early period was not much different from later values, but in a less intensive fishery relying more on fish of greater ages (Christie 1978), the gill nets may have selected for the largest members of the recruiting year-class.

In strictly statistical terms it can be argued there was no compensatory growth effect associated with the whitefish stock decline. The relevant multiple regression equation is:

$$(5) \quad \hat{Y} = 0.8878 - 0.12791\, X_1 + 1886\, X_2 \cdot 10^{-8}$$

where Y = June–September age IV growth increment (Fig. 8)

X_1 = corrected wound incidence for the nine data pairs of Fig. 8.

X_2 = whitefish population values of Fig. 8.

The slope of the line for increment on wound incidence with population constant is significantly different from zero ($t = 6.97$, $P < 0.01$). By contrast the slope for increment on population with wound incidence constant is very small ($t = 0.79$, $P \simeq 0.5$).

The results of this analysis can be challenged on the basis of the short series of years involved. Growth increases caused by the whitefish density declines in the final years of the series might not have been discernible, given measurement error and the evidently strong effect of the lamprey wounding. It is particularly unfortunate that the more sporadic fishing of the latter 1960s broke the continuity of sampling and prevented calculation of the increments for all years. Fish of all ages were conspicuously larger in that period. The question concerning the recent years should be answerable when we are able to study the growth of survivors from a proposed whitefish stocking program. No definitive answer will emerge for the early period, however, and we are limited to the inference that the age IV–VI scallop probably indicates that there was a lamprey mortality effect in that period.

The evident severity of the lamprey impact on seasonal growth was surprising in view of the known intensity of the whitefish fishery (Christie 1968, 1978). The simplest explanation is that the fishery took more fish than the lamprey but exerted its size-selective effect more evenly across the summer. Thus if the average size of fish in a June sample were small by reason of fishing intensity, the September sample would likely have had a small average size for the same reason. The lamprey impact had a greater effect on the size of the fish because it came at the end of the summer, and because fishing had already significantly reduced fish abundance.

If exploitation pressure were such as to reduce the stock density more than usual, one might expect more lamprey wounds and a smaller size increment. This effect could not be discerned in the data, and in fact the reverse tendency appeared. The correlation coefficient for wounding on exploitation rate (Table 6) was −0.42 and for size increment on exploitation rate (Fig. 8, Table 6), 0.49. Neither of these values is statistically significant. Our tentative explanation is that exploitation rate was steady through time, in a relative sense, compared with the sharp decrease in wounding, and sharp increase in whitefish size increment. Any possible effect would be further confounded by the fact that the exploitation statistics represent averages for the full year, and spring removals by the fishery could be especially important.

Tentative conclusions from this section are that:

a) Normally growing fish which escape lamprey attack or survive attacks at smaller sizes have increasingly better chances of surviving from age VII and about 1250 g onwards.

b) The lamprey:whitefish size ratio may be the critical factor in determining when lamprey wounding ceases to be an important mortality factor.

c) Small whitefish probably succumb to attack more readily but are less likely to be attached.

d) Mortality induced by sea lamprey attacks was significant in August, but the data sugest that, while size selectivity is very evident in the lamprey wound incidence data, the effect of wounding on growth increment is exaggerated by the fact that the lamprey impacted on much reduced late summer fish populations.

e) In this case lamprey abundance was prey-limited, and survival of individual lampreys may have been more important in determining growth rate than density-dependent growth.

f) Different prey species alter lamprey growth, and probably survival as well.

g) Fish are wounded after capture in gill nets and this factor should be taken into account where any trend in set duration through time can be discerned.

Discussion

The suggestion that sea lamprey migrate over long distances in Lake Ontario is an interesting one. Applegate and Smith (1951) found that tagged lamprey could move over distances as great as 240 km, but the notion of regularly used summer feeding grounds distant from the stream of origin raises the question as to how such migrations could happen. Even with random dispersal, the lamprey seems such a weak swimmer that energetics would argue against long migration in a short time period. We know no fish stocks, moreover, which would provide a vectoring system. Boats have acted to move lamprey between and within lakes, but the overall importance of these is not understood. However, even if one allows the lamprey the strength and inclination to swim long distances, what is the nature and precision of the guidance system which must be involved?

Precision movements and homing could offer a partial explanation for the long delay involved in the penetration of the sea lamprey to the upper Great Lakes, but the possibility of wide dispersal of large numbers of animals makes the delay more puzzling. It has been conventional wisdom for many years (Smith 1971) that the time lag between the opening of the Welland Canal in 1829 and the first reports from Lake Huron and Lake Michigan in 1936 and 1937 (Applegate 1950) arose because Lake Erie was climatically inhospitable for sea lampreys (i.e. streams were too warm for reproduction). This implies that the animal had to be established in Lake Erie and produce local generations which could finally make the migration to Lake Huron, or perhaps, that sea lamprey migrate in summer when the warm waters of western Lake Erie would prove an effective obstacle to migration. The two ideas are not mutually exclusive, and both could have been factors. We suggest, however, that neither contention is based in fact and it is quite possible that ship traffic in the fall or spring could have carried sea lamprey from Lake Ontario to Lake Huron during the last century. Such a spread would have been more likely with extravagant lamprey production, but not impossible with close homing and periodic large stream outputs.

The summer maximum for lamprey predation on whitefish is paralleled in the observations on planted lake trout in Lake Ontario. The cycle in Lake Superior on the other hand, is the reverse, with lamprey wounding high in spring and fall (A. H. Lawrie, OMNR, Maple, Ont., personal communication). The most likely explanation relates to the generally accepted view that the parasitic life of at least some of the Lake Superior animals is more than 2 yr long. Spawning occurs later in the north, and while it is underway, lakeward predation is carried on by the lamprey which are residual in the lake. By fall the new generation of transformed animals swells the population and the elevated wound frequencies continue until the next spring when the sexually maturing animals leave the lake for the spawning streams. This life history pattern places a constraint on the level of lamprey population reduction attainable by chemical control. It is argued, similarly, that the simple life history of the sea lamprey in Lake Ontario should permit more complete control when all river sources of lamprey have been identified and treated.

The apparently contagious distribution of lamprey wounds within sample catches of prey fish emphasizes the need for rigorous sampling designs and extensive data collection for the analysis of trends in sea lamprey abundance. Sampling clearly must be sufficiently intensive to account for all of the important variables discussed in this work. At low levels of lamprey density and/or improved levels of prey density it is very difficult to obtain samples sufficiently large to confirm statistically small temporal changes in the predator:prey ratios, and in this circumstance the need for a rigidly systematic sampling program to provide ongoing assessment of the success of control is increased.

There is a hypothesis which goes further towards reconciling both the lapse in invasion time and the lack of evidence of predation impact in Lake Ontario during the last century, than either of the two discussed at the beginning of this paper. This is the hypothesis that the critical factor limiting distribution is low stream temperature, and its author is A. H. Lawrie (Min. Nat. Res., Maple, Ont., personal communication). According to this postulation the mean 60°F (15.5°C) July air temperature isotherm provides an approximate northern limit to the present stream distribution of sea lamprey ammocoetes. If this can be confirmed it is not difficult to see an influence of past climatic change in the colonization of the upper lakes. May (1979) has recently summarized a great deal of the voluminous recent paleoclimatic literature, reminding us of the well-known "Little Ice Age" which spanned the period 1600–1850, and also of the ensuing upswing to warmer conditions which became particularly noticeable by 1915 and reached its peak around 1940. Cooler water temperature in Lake Ontario tributary streams, which allowed brook trout (*Salvelinus fontinalis*) distribution to extend to the mouths of the streams in the early postsettlement years, has been attributed (Christie 1972) to the forests of the watershed, which had been largely removed by the middle of the 19th century; while this factor cannot be discounted, the cool climatic conditions of the era equally deserve attention. Christie (1968) attributed the disappearance of a mid-19th century seine fishery at Prince Edward County in Lake Ontario to overfishing. This may have been the case but a point overlooked was that the fishery was pursued during September each year, and lake water temperature conditions in recent years, at least, would have prevented whitefish from coming close to shore at that season. Similarly, there has been an extraordinary faunal shift in southern Ontario since the turn of the century and it was characterized by northward range extensions of many mammals and birds. The eastern gray squirrel (*Sciurus carolinensis*), coyote (*Canis latrans*), and quail (*Colinus virginianus*) are a few well-known examples. If the lamprey distribution is indeed limited by climate, the 60° isotherm was unquestionably further south in the last century, with the possible effect that the Lake Ontario habitat was marginal, and the upper Great Lakes probably outside the range entirely. The especially important consideration is that the already established return from the warm conditions of the early part of this century towards conditions closer to the long-term climatic norm (May 1979) could make sea lamprey control in the upper Great Lakes somewhat easier in future. This line of speculation invites more critical and detailed studies of the present distribution of the sea lamprey in the Great Lakes.

The data presented here strongly implicate the sea lamprey as a mortality factor in the eastern Lake Ontario whitefish stocks. The observation that the whitefish apparently began to survive lamprey attacks better beyond about 1250 g (age VII) accords well with the experimental results reported by Farmer et al. (1975). By their reckoning a salmonid of this size could replace 3.8 g of blood per day (10% of blood volume) and a 29-g lamprey would take 3.5 g of blood per day (12% of body weight per day). Growth of lamprey from this size to the mid-September size of 50 g would have had the effect of making the older fish liable to fatal attack for a shorter period of time than younger fish, and of course, fish surviving this marginal year to age

VIII and beyond would have gained a great deal of resistance to the lamprey. Very few fish younger than age VII exceeded the 40:1 wet weight for wet weight ratio and those that did not survive to cross this threshold must have nearly all succumbed to lamprey attack, as suggested by the data presented here.

One apparent inconsistency in the picture offered by these data is illustrated in Fig. 6. If the high average length of the wounded fraction of the whitefish catch sample reflected selective mortality of the small fish attacked in the early years, when fish were abundant and small, why would the lines in Fig. 6 not converge in the later years as the fish became scarcer and larger? In other words, given that larger fish survive better to appear more frequently in the catch as wounded fish, the wounded segment of the population should have produced a higher general wound incidence, and, occupying a broader segment of the length distribution, should have produced average length values closer to those of the unwounded part of the sample. Our interpretation is that in the years beyond the termination of the lamprey collections (1964) the availability of large prey produced larger lamprey (if fewer of them) and the relative mortality impact remained the same. The matter clearly cannot be resolved with the present data, but it is hoped that the postulated coupling of prey-controlled lamprey mortality and prey-size limited lamprey growth will stimulate further discussions and investigation. The point of immediate concern is that the accepted method of presenting lamprey wound incidence data for individual size-classes in the Great Lakes may act to overestimate lamprey abundance in either falling or rising conditions of prey abundance. Now that wounds can be more clearly distinguished from incipient scars and interrupted attacks possibly distinguished from completed ones (King 1980), future studies can be more readily directed towards these questions.

There was little doubt that the Lake Ontario whitefish failed because reproduction was interrupted by environmental factors (Hurley and Christie 1977), but one wonders if the stock could have persisted if that had not been the case. The implication from the data presented here is that the fishery kept ahead of the lamprey by reason of its season and its intensity. By catching fish younger through its intensification (Christie 1963) the fishery acted to limit the absolute numbers of whitefish surviving to reach the 1250-g threshold before August each year. It is possible that larger numbers of large fish could have acted to reduce predation and mortality among the smaller fish. It seems equally likely, however, that improvements in lamprey survival would have acted to maintain mortality levels in smaller fish, at least. This would have been especially true if, as surmised, the more energetically efficient feeding on large fish produced larger lamprey and thus a higher incidence of fatal attacks among larger fish. There is also a (theoretical) level of lamprey density where multiple wounds could raise mortality levels in larger fish. We feel that the weight of the evidence suggests that in the absence of a fishery, lamprey impact would have equilibrated at some lamprey:fish size ratio. Given the presence of the fishery, therefore restricting the level of its catch would have likely only given more fish to the sea lamprey.

The whitefish case was special in that it was a simple predator:prey system. It is interesting to consider, however, what would have happened if alternate prey had been available in significant abundance during the period of this study. We infer that the presence of large salmonids would relax predation pressure on the whitefish, but as in the scenario discussed above, we wonder if the presence of more large lamprey might not have acted to maintain elevated mortality levels in the whitefish even as a more incidental prey. It seems likely that sea lamprey growth has an upper limit in the Great Lakes, and while this would protect some salmonids, it would not help whitefish. The largest specimens seen by Dymond et al. (1929) were 179 g in autumn and this is close to the size of spawning-run lampreys (184 g) at the Ocqueoc River, Lake Huron, in 1947 (Smith 1971). If we accept the 40:1 ratio concept these levels suggest that lamprey would only be innocuous where large numbers of prey, which exceeded 7 kg in weight, were present. The general observation in the Great Lakes as well as Lake Ontario has been that whitefish are not heavily utilized by lamprey until lake trout and burbot densities are much reduced, so we infer that the feeding preferences of the sea lamprey acted to protect the whitefish. Whitefish and probably white suckers as well should not be regarded as buffer species in a lamprey:trout system.

We take it that the scar accrual data of Fig. 5 confirm the laboratory observations of Farmer et al. (1975), and support the hypothesis that sea lamprey in fact do equilibrate as a parasite, in conditions of large host size, and high density. The observations here further suggest that in the past, periodic natural reductions in size and numbers of the natural hosts could have acted to limit lamprey density.

At the outset we indicated that the question of relevance to Great Lakes sea lamprey problems was whether natural (i.e. environmental) controls over sea lamprey numbers, or predator–prey accommodations figured most prominently in stabilization of sea lamprey numbers. In our review of the data we felt that the latter consideration was of great importance. The time lag involved in the invasion of the upper Great Lakes by the lamprey, and its evidently benign role in Lake Ontario during the last century, however, led us increasingly to the view that there must have been natural density controls, and of those the climatic hypothesis was the most appealing. We feel then, that both effects were at work in Lake Ontario, and believe that, more generally speaking, it was the fishery that acted to disengage the biotic control mechanisms.

The likelihood of equilibrium leads to consideration of use of fishery management procedures to ameliorate sea lamprey control costs. Instead of encouraging fisheries to take the largest fish — the traditional approach, it might be feasible to apply exploitation pressure to middle-sized fish, while maintaining a large pool of large, older fish to absorb lamprey parasitic pressure. In this paper we have stressed the importance of further research, and this area of natural equilibrating mechanisms is perhaps the most deserving of intensive investigation. As we have also tried to demonstrate, it also represents the most difficult area to research. The unquestionably high costs of such studies have probably not been justifiable in the past, but given the soaring costs of lampricide and other considerations which gave rise to SLIS, perhaps major future investment can now be contemplated.

Acknowledgments

The early stimulus for the Lake Ontario sea lamprey studies came from the Federal–Provincial Great Lakes Fisheries Committee, which was the coordinating body concerned with lamprey control and research up to the time of formation of the International Great Lakes Fishery Commission. The work was supported throughout by the Ontario Department of Lands and Forests (now the Ontario Ministry of Natural Resources), and we are grateful for the willingness of the agency to support long-term ecological investigations of the sort described here.

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Applegate, V. C. 1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 55: 237 p.

Applegate, V. C., and B. R. Smith. 1951. Movement and dispersion of a blocked spawning run of sea lampreys in the Great Lakes. Trans. N. Am. Wildl. Conf. 16: 243–252.

Aron, W. I., and S. H. Smith. 1971. Ship canals and aquatic ecosystems. Science 174(4004).

Beamish, F. W. H. 1980. Biology of the North American anadromous sea lamprey (*Petromyzon marinus*). Can. J. Fish. Aquat. Sci. 37: 1924–1943.

Beamish, F. W. H., and I. C. Potter. 1972. Timing of changes in the blood, morphology and behaviour of *Petromyzon marinus* during metamorphosis. J. Fish. Res. Board Can. 29: 1277–1282.

Bliss, C. I., and R. A. Fisher. 1953. Fitting the negative binomial distribution to biological data and note on the efficient fitting of the negative binomial. Biometrics 9: 176–200.

Christie, W. J. 1963. Effects of artificial propagation and the weather on recruitment in the Lake Ontario whitefish fishery. J. Fish. Res. Board Can. 20: 597–646.

1968. Possible influences of fishing in the decline of Great Lakes fish stocks. Int. Assoc. Great Lakes Res. Proc. 11th Conf. Great Lakes Res. 1968: 31–38.

1972. Lake Ontario: effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 913–929.

1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Board Can. 31: 827–854.

1978. A study of freshwater fishery regulation based on North American experience. FAO Fish. Tech. Pap. 180: 46 p.

Christie, W. J., and H. A. Regier. 1973. Temperature as a major factor influencing reproductive success of fish — two examples. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 164: 208–218.

Crossman, E. J., and H. D. Van Meter. 1979. Annotated list of the fishes of the Lake Ontario watershed. Great Lakes Fish. Comm. Tech. Rep. 36. 25 p.

Dymond, J. R., J. L. Hart, and A. L. Pritchard. 1929. The fishes of the Canadian waters of Lake Ontario. Univ. Toronto Stud. Biol. Ser. 33: 35 p.

Farmer, G. J., F. W. H. Beamish, and G. A. Robinson. 1975. Food consumption of the adult landlocked sea lamprey *Petromyzon marinus* L. Comp. Biochem. Physiol. 50A: 753–757.

Gage, S. H. 1928. The lampreys of New York — life history and economics, p. 158–191. *In* Biological survey of the Oswego River system. Suppl. 17th Ann. Rep. N.Y. Cons. Dep.

Greeley, J. R. 1939. A biological survey of the Lake Ontario watershed. N.Y. Suppl. 29th Ann. Rep. XVI: 1–261.

Hurley, D. A., and W. J. Christie. 1977. Depreciation of the warmwater fish community in the Bay of Quinte, Lake Ontario. J. Fish. Res. Board Can. 34: 1849–1860.

Johnson, B. G. H., and W. C. Anderson. 1980. Predatory-phase sea lampreys (*Petromyzon marinus*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37: 2007–2020.

King, E. L. jr. 1980. Classification of sea lamprey (*Petromyzon marinus*) attack marks on Great Lakes lake trout (*Salvelinus namaycush*). Can. J. Fish. Aquat. Sci. 37: 1989–2006.

Lapworth, E. D. 1956. The effect of fry plantings on whitefish production in eastern Lake Ontario. J. Fish. Res. Board Can. 13: 547–558.

Lark, J. G. I. 1973. An early record of the sea lamprey (*Petromyzon marinus*) from Lake Ontario. J. Fish. Res. Board Can. 30: 131–133.

Lett, P. F., F. W. H. Beamish, and G. J. Farmer. 1975. System simulation of the predatory activities of sea lampreys (*Petromyzon marinus*) on lake trout (*Salvelinus namaycush*). J. Fish. Res. Board Can. 32: 623–631.

May, R. M. 1979. Arctic animals and climatic change. Nature 281: 177–178.

Paloheimo, J. E. 1961. Studies on estimation of mortalities I. Comparison of a method described by Beverton and Holt and a new linear formula. J. Fish. Res. Board Can. 18: 645–662.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

Siegel, S. 1956. Nonparametric statistics for the behavioural sciences. McGraw-Hill Book Company, New York, NY.

Smith, B. R. 1971. Sea lampreys in the Great Lakes of North America, p. 207–247. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London.

Smith, S. H. 1970. Species interactions of the alewife in the Great Lakes. Trans. Am. Fish. Soc. 99: 754–765.

Response of Lake Whitefish (*Coregonus clupeaformis*) to the Control of Sea Lamprey (*Petromyzon marinus*) in Lake Huron[1,2,3]

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Changes in population parameters of three stocks of whitefish (*Coregonus clupeaformis*) in Lake Huron following control of sea lamprey (*Petromyzon marinus*) have varied between the major basins of the lake. In the North Channel and main basin, whitefish survival rates increased significantly, from values of 23 to 37% and 16 to 24%, respectively. In both areas the abundance of lamprey declined while whitefish increased. In Georgian Bay, whitefish populations did not reflect changes attributable to lamprey control, possibly because of low lamprey abundance. During the control period, whitefish survival rates declined from 57 to 39%, abundance declined and growth rates increased.

Key words: Lake Huron whitefish, lamprey control, *Petromyzon marinus*

SPANGLER, G. R., AND J. J. COLLINS. 1980. Response of lake whitefish (*Coregonus clupeaformis*) to the control of sea lamprey (*Petromyzon marinus*) in Lake Huron. Can. J. Fish. Aquat. Sci. 37: 2039–2046.

Les changements qui se sont produits dans les paramètres de population de trois stocks de grands corégones (*Coregonus clupeaformis*) dans le lac Huron par suite du contrôle de la grande lamproie marine (*Petromyzon marinus*) ne sont pas les mêmes dans les principaux bassins du lac. Dans le chenal du Nord et le bassin principal, le taux de survie du grand corégone a augmenté de façon significative, passant de 23 à 37% et de 16 à 24% respectivement. Dans les deux régions, le nombre des lamproies diminua à mesure qu'augmentait celui des grands corégones. Les populations de grands corégones de la baie Georgienne ne subirent pas de changement attribuable au contrôle de la lamproie, possiblement à cause d'une faible abondance de cette dernière. Pendant la période de contrôle,le taux de survie du grand corégone passa de 57 à 39%, son abondance diminua et les taux de croissance augmentèrent.

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EFFECTIVE chemical control methods (Applegate et al. 1961) for sea lampreys, *Petromyzon marinus*, have been applied to tributaries in the Great Lakes watershed for over two decades (Smith and Tibbles 1980), and the effects of the control procedures are documented for both lampreys (Heinrich et al. 1980; Schuldt and Goold 1980) and resident and anadromous teleosts (Dahl and McDonald 1980). This paper describes changes in population parameters of several stocks of lake whitefish, *Coregonus clupeaformis*, in Canadian waters of Lake Huron which have been under study by the Ontario Ministry of Natural Resources since 1958, before and during chemical control.

Assuming that lampreys increase the mortality rate of their hosts, we postulate that, in the case of whitefish, the prey responses would be similar to those of commercially exploited populations (Regier and Loftus 1972). Therefore, when lamprey abundance was reduced we would expect to observe the following changes in prey populations: a reduction in mortality and wounding rates, increased abundance and reduced growth rates. Healey (1975, 1978) has proposed that growth rates are indicators of predation (especially fishing) on whitefish and lake trout (*Salvelinus namaycush*), assuming a density dependent effect. We recognize that increased fishing pressure may mask the effect of reduced lamprey predation.

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TABLE 1. Sources of data on lampreys and prey species from the North Channel (NC), Georgian Bay (GB), and main basin of Lake Huron (LH).

Type of information	Period	Area	Source
Whitefish catch and effort statistics	1950–65	GB	Cucin and Regier (1966)
	1966–75	GB	Commercial Fisheries Repts. (Ontario Form CF.1)
	1958–75	NC	Commercial Fisheries Repts.
	1958–75	LH	Commercial Fisheries Repts.
Miscellaneous species catch	1961–65	All	Anon. (1972a)
	1966–70	All	Anon. (1972b)
	1971–75	All	Ridgley (1976)
Whitefish catch samples (age, size, and lamprey marks)	1958–75	LH	Lake Huron Research Unit[a]
	1958–74	NC	Lake Huron Research Unit
	1975	NC	Lake Huron Assessment Unit[b]
	1956–64	GB	Cucin and Regier (1966)
Tagged whitefish	1964–68	LH	Spangler (1974)
	1969–77	LH	Lake Huron Research Unit
Lamprey trapped at assessment barriers	1965–75	All	Great Lakes Fishery Commission, annual reports

[a] Ontario Ministry of Natural Resources, R.R. 1, Tehkummah, Ont. P0P 2C0.
[b] Ontario Ministry of Natural Resources, 611 Ninth Ave. E., Owen Sound, Ont. N4K 3E4.

Materials and Methods

We examined data (from several sources, Table 1) for evidence of the effect of lamprey upon fish populations in three areas of Lake Huron (Fig. 1). We have relied upon the catch and effort statistics in official reports (Ontario Form CF.1) submitted by licensed fishermen in each area. Monthly reports of whitefish catches in gill nets were individually tabulated for most fishermen known to provide reliable accounts of operations in Statistical Districts OH-1 (south Manitoulin Island shore of main basin), NC-1 (North Channel waters), and GB-4 (southern Georgian Bay) (see Smith et al. 1961 for area boundaries).

Gillnet catches rather than catch per unit of effort (CUE) data are utilized directly to represent changes in abundance of whitefish. In this study, catches are significantly correlated with CUE for each District ($r = 0.838$, $P < 0.001$; $r = 0.699$, $P < 0.001$; and $r = 0.787$, $P < 0.001$ for Districts OH-1, NC-1, and GB-4, respectively). Although effort data are not available for "alternate prey" species sought by the commercial fishery, we assume that catch values for these species (cisco, *Coregonus artedii*, round whitefish, *Prosopium cylindraceum*; and chub *Coregonus* spp.), also represent their relative abundance. Data for suckers (*Catostomus* spp.), which are largely incidental catches, are less precise but represent the only available estimates of abundance. In the late 1960s gear efficiency improved in Districts NC-1 (Collins 1979) and GB-4 with the use of monofilament gill nets in the whitefish fishery. This change has probably inflated the estimate of abundance for whitefish in those areas. However, in northern Lake Huron (District OH-1) the major fishery at Burnt Island did not use monofilament web extensively during the study period.

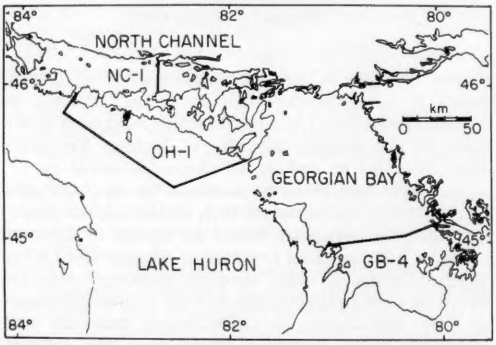

FIG. 1. Upper Lake Huron showing locations of three statistical districts, North Channel (NC-1), northern Lake Huron (OH-1), and southern Georgian Bay (GB-4) for which commercial fish landings are reported by Ontario Ministry of Natural Resources. Site of Burnt Island (BI) fishery is indicated by dot in OH-1.

Commercial catches were routinely sampled throughout the study period. A minimum sample for an individual whitefish involved a fork-length measurement, removal of scales for aging purposes and examination for evidence of lamprey attack. All age determinations were made from scale impressions on acetate slides.

Total survival rates for each of the areas were estimated from the age composition of the catches. Since year-class strength of whitefish in the Great Lakes is known to vary considerably between years (Cucin and Regier 1966; Christie 1963), we combined as many years of data as possible for each area and time period before estimating the least squares regressions. We also estimated survival rates using the method of Robson and Chapman (1961) for comparison with the least squares (catch curve) estimates.

Growth rates were determined by computing average lengths of whitefish of each age-class sampled in the large-mesh gillnet fisheries of each area in the spring (April–May) before the onset of seasonal growth in June. Mesh sizes of the gill nets (114 mm, stretched measure) employed within areas have not varied during the study, so corrections for gillnet selectivity were not used.

Classification methodology for lamprey-inflicted marks remains a subject of some debate for several species of prey

TABLE 2. Estimates of total survival and mortality for Lake Huron whitefish before and after lamprey control.

				Total survival Catch curve method		Robson and Chapman (1961)
Area	Lamprey control	Sample years	Age-classes	$\hat{s}$	r	A[a]
GB	Before	1958–62	8–14	0.572	−0.949	0.460
GB	After	1965–74	5–10	0.386	−0.992	0.604
(Ancova $F = 25.29,9,1$ df, $P < 0.005$ where $n = 24\,846$)						
NC	Before	1958–62	3–8	0.228	−0.992	0.803
NC	Partial	1963–67	3–8	0.306	−0.990	0.696
NC	After	1968–75	4–8	0.366	−0.998	0.652
($F = 25.05,12,2$ df, $P < 0.001$, $n = 37\,368$)						
LH	Before	1964–70	4–9	0.162	−0.990	0.874
LH	After	1971–75	4–9	0.240	−0.996	0.768
($F = 12.81,10,1$ df, $P < 0.005$, $n = 27\,641$)						

[a] Where A = total annual mortality rate and r is the correlation coefficient.

fish (King 1980). In the case of whitefish, lamprey marks were classified as wounds and scars; the former corresponds to what Lennon (1954) called "new wounds" which are characterized by a break in the fish's skin and no evidence of healing. Our "scars" correspond to Lennon's "old wound" category, i.e. evidence of healing ranging from peripheral scar tissue to complete glazing or closure of the wound.

Changes in the incidence of lamprey marks on prey fish may reflect either the abundance or the feeding activity of lampreys or variation in prey abundance (Berst and Wainio 1967; Hall and Elliott 1954; Berst and Spangler 1970; Spangler 1970). Fresh wounds also provide a more direct indicator of "current" lamprey activity than do healed scars which may be the result of several months or years of accumulated attacks on an individual fish.

Chemical control of sea lampreys in Lake Huron began in 1960. The treatment schedule (see Smith and Tibbles 1980) during the early 1960s was intermittent but, by 1966, most streams were being treated on a 4-yr cycle. Southern Georgian Bay (GB-4) streams were first treated in the fall of 1960 and spring of 1961 and various streams were treated again in 1968, 1970, 1972, and 1976. Treatment of North Channel streams (NC-1 and adjacent areas) commenced in 1961 and re-treatment of most streams occurred in 1966–67, 1970–71, and 1974–75. Main basin streams (study area in OH-1) were treated in 1969, 1973, and again in 1977. Because of variation in the treatment schedule between areas, the fish samples from each area are analyzed separately. Further, data on tag returns for southern Georgian Bay (Cucin and Regier 1966) and at Burnt Island (Sprangler 1970) indicate that whitefish stocks in these areas are discrete.

Discussion of the influence of sea lampreys upon fish stocks has been divided into a pretreatment and a posttreatment period for each area. We define the pretreatment periods as those years before the earliest application of chemical toxicant (TFM) to lamprey-producing tributaries in each area. We recognize that lamprey control efforts in the upper lakes date from the late 1940s and that substantial numbers of migrating sea lampreys were killed at electrical and mechanical barriers during the early years of the program. However, our data series on prey fishes do not go back that far.

Results

WHITEFISH SURVIVAL

Total annual survival rates of whitefish increased significantly during the posttreatment period in the North Channel and Lake Huron but declined in southern Georgian Bay (Table 2). Based on the catch curve method, survival rates in the North Channel have increased from 23 through 31 to 37% since the onset of lamprey control. Furthermore there has been an increase from age 3 to 4 in the modal age of the catch, consistent with improved survival. We also estimated survival from data corrected for improved gear efficiency which occurred with the introduction of monofilament nylon gill nets during 1969–74 (Collins 1979). In this analysis, catch curves based on catch per unit of effective effort (data not shown) yielded survival values of 21, 27, and 32%, respectively, for the time periods. Although the estimates differ slightly, both show similar trends and are consistent with total mortality rates estimated by the method of Robson and Chapman (1961).

In the main basin of Lake Huron (District OH-1, Fig. 1) total annual survival increased from 16% during the pretreatment period to 24% following lamprey control. Estimates for the earlier period are consistent with those reported for tagged whitefish in the Burnt Island area (Spangler 1974). There has been a very slight increase in the modal age at Burnt Island since lamprey control, and a slight broadening of the population's age structure. Since total fishing effort in this area has increased since 1969 with no significant changes in gear efficiency, we suggest that the increased survival is related to reduced lamprey predation.

In contrast, survival rates for Georgian Bay whitefish declined from 57 to 39% in the posttreatment period but continue to be higher than in the other areas (Table 2). Our confidence in this observed change is

TABLE 3. Proportion of whitefish catch wounded in each area (Y) in year (n) on the numbers of adult lamprey (X) returning to assessment barriers in year ($n + 1$). *Significant at 95% level; **Significant at 99% level (t-test).)

Area[a]	Assessment barrier	Equation	Corr. Coef.
LH	Manitou R.	$Y = 2.70+0.0279X$	0.915**
LH	Blue Jay Cr.	$Y = 1.00+0.0109X$	0.824**
LH	Bayfield R.	$Y = 2.42+0.0247X$	0.901**
LH	Ocqueoc R.	$Y = 5.30+0.0009X$	0.143
LH	Kaskawong Cr.	No regression	0.030
GB	Still R.	$Y = 0.0654+0.0005X$	0.898**
GB	Naiscoot-Harris R.	$Y = 0.0790+0.0011X$	0.640*
GB	Mad R.	$Y = 0.242+0.0042X$	0.713*
NC	Kaskawong Cr.	$Y = 3.26-0.0016X$	−0.086

[a]LH, Lake Huron main basin; GB, southern Georgian Bay; NC, North Channel.

strengthened by the generally close agreement of our estimates with those of Cucin and Regier (1966) which were based on population estimates of tagged fish. Also, the decrease from age 8 to 5 in the modal age of the catch from southern Georgian Bay, is consistent with reduced survival rates. However, the principal reason for the high survival rate in the pretreatment period is the presence of a series of year-classes of slow growing fish which did not recruit to the gear until age 8 or older. In this particular case the evidence neither supports nor refutes our basic premise.

LAMPREY ABUNDANCE

To determine if there is a relationship between lamprey abundance and wounded fish in the catch, we regressed the frequency of wounded fish in the August–November period (dependent variable) on runs of adult lampreys (independent variable) to assessment barriers the following spring and summer. The percentage of wounded fish in the catch was significantly correlated with the abundance of lampreys for those fish captured adjacent to the lamprey producing tributaries (Table 3). However, there was no correlation between available data on runs of lampreys in the Ocqueoc River, Michigan, and proportion of wounded fish from the south Manitoulin shore (immediately opposite the Ocqueoc). Similarly, runs of lampreys to Kaskawong Creek at the west end of the North Channel do not correlate well with wounding frequencies of whitefish from more easterly areas of the North Channel or along the south Manitoulin shore.

These observations indicate that the wounding rate is probably related to lamprey abundance and also that parasitic-phase lampreys segregate into discrete groups within the lake. This is consistent with Johnson's (1969) suggestion (supported by growth data) that lampreys become associated with groups of prey fish early in the season and remain with them throughout the summer growth period. The obvious corollary to this proposition is that the fish communities in various parts of the lake are likely to respond to lamprey control independently (if at all) in accordance with local lamprey activity.

Lamprey-wound frequencies on whitefish of commercial size vary seasonally with a major peak in August and September (Fig. 2). This peak corresponds seasonally with the maximum growth of sea lampreys (Johnson and Anderson 1980) and maximum lamprey feeding activity in the laboratory (Parker and Lennon 1956). There is also a tendency for higher wounding frequencies among the larger (or older) fish of several species (Berst and Wainio 1967; Berst and Spangler 1970; Budd and Fry 1960; Collins 1971). This is consistent within the different basins of Lake Huron but contrary to Maitland's (1980) observations at Loch Lomond. To provide the greatest reliability in comparisons of wounding frequency between years, our analysis is based upon lamprey wounds observed on whitefish during the late summer and fall seasons.

The incidence of lamprey-wounded whitefish in the North Channel and Lake Huron began declining prior to chemical control and continued to decline following the onset of treatments (Fig. 3). We infer from this that lamprey abundance and predation declined sufficiently in these areas to elicit a response in the whitefish populations. In contrast, in southern Georgian Bay the incidence of wounded fish was less than 1% except for 2 years during the study suggesting that lamprey were probably not a significant predator of whitefish there. We would not expect to observe a significant response in whitefish to lamprey control.

PREY ABUNDANCE

Trends in commercial catches of whitefish during 1958–77 (Fig. 4, panel B) and alternate prey species (panel A) during 1961–75 in each study area were examined as abundance indices (see methods), to evaluate possible responses to lamprey control. Although the relative abundance of whitefish fluctuated in each area, there has been a moderate increase of

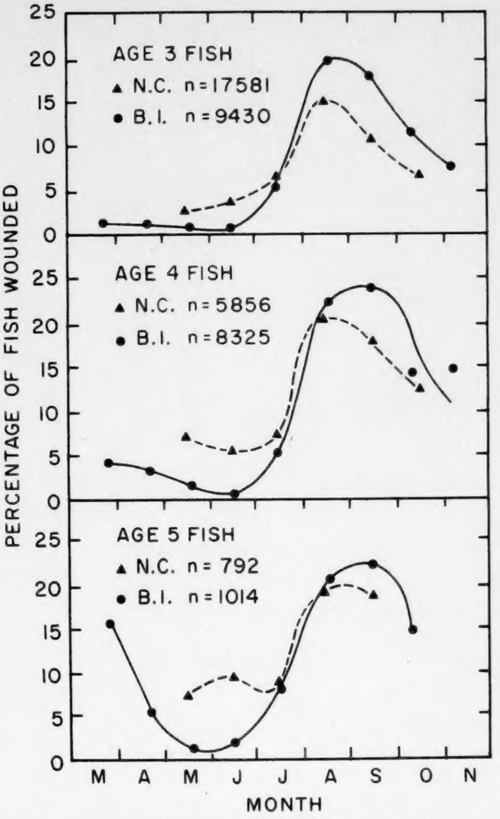

FIG. 2. Seasonal incidence of wounded whitefish from the Burnt Island (B.I.) fishery during 1964–66 (redrawn from Spangler 1970), solid lines, and the North Channel (N.C.) fishery during 1958–67, dotted lines.

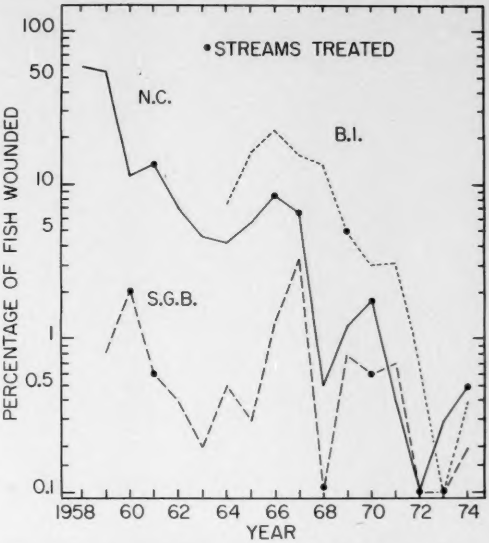

FIG. 3. Annual incidence of wounded whitefish during Aug.–Nov. period; 14 400 fish examined in the North Channel (N.C.), 15 308 in southern Georgian Bay (S.G.B.), and 24 249 in the Burnt Island (B.I.) area of northern Lake Huron. Treatment years for local major streams are indicated by dots on the curves. The log scale is not used for statistical purposes, only as a convenience to show low percentages.

fish (vulnerable to gill nets) in the North Channel, a large increase in northern Lake Huron, and a decline in southern Georgian Bay during the postcontrol period. Peaks in catches reflect the recruitment of year-classes and are not synchronous between areas nor do they appear to be directly related to stream treatment. In the main basin of Lake Huron, whitefish increased in abundance prior to stream treatment.

Chub landings (upper curve, panel A) rose to a record level in the Canadian waters of Lake Huron in 1961 (Berst and Spangler 1973) but did not peak in northern Lake Huron (OH-1) until 1965. Stocks subsequently declined to minimal levels by 1970. Chubs were numerically the most abundant species in Georgian Bay from 1958 to 1963 (Craigie 1971), but were considered to be of poor commercial quality. Georgian Bay chubs were fished more intensively as alternate stocks declined and by 1978 abundance had fallen to very low levels in southern Georgian Bay (N. R. Payne, Lake Huron Fisheries Assessment Unit, Owen Sound, Ont., personal communication). Chubs are important prey for lampreys in the Great Lakes (Johnson and Anderson 1980). Their availability as alternate prey was much greater in Georgian Bay throughout this study and in Lake Huron before 1965 than in the North Channel, where they were not harvested commercially, but were frequently taken in experimental gill nets (Collins 1964).

Sucker stocks (primarily *Catostomus commersoni*) (lower curve, panel A) have apparently not changed appreciably in northern Lake Huron and Georgian Bay, but they have increased in abundance in the North Channel — so much so that whitefish fishermen there now use larger mesh (127 mm rather than 114 mm stretched measure) nets to avoid them. Suckers are the principal alternate prey of lampreys inhabiting the North Channel, and their abundance relative to the size of the lamprey population may have influenced the frequency of lamprey wounds on whitefish there and elsewhere.

On balance, during the postcontrol period, whitefish abundance has increased in the North Channel and in Lake Huron has continued an upward trend which

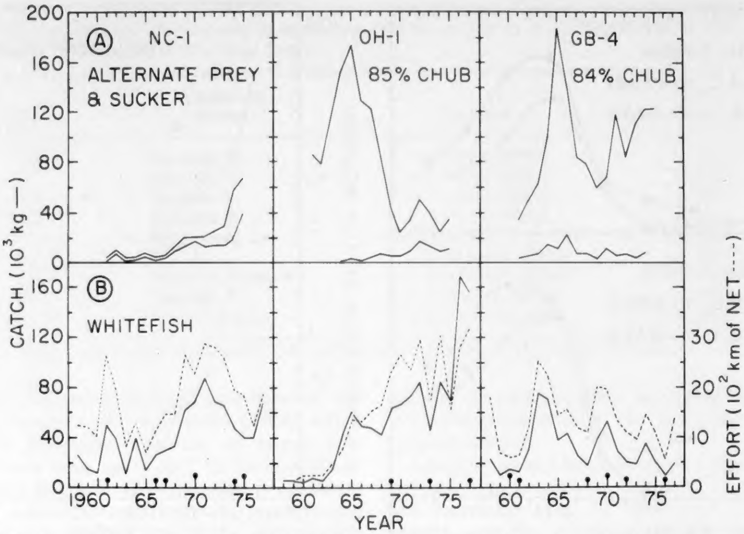

FIG. 4. **Annual commercial gillnet landings and netting effort for whitefish computed from CF.1 reports (panel B) and reported landings of chubs and suckers (lower line) during 1961–75, from O.M.N.R. Fisheries Branch reports 1972 and 1976 (panel A). Chemical treatment years for major local streams are indicated by dots on the abscissa.**

began before lamprey control — responses we anticipated to occur with the reduction of lamprey predation. Georgian Bay fish have not demonstrated any response attributable to lamprey control.

GROWTH RATES

Assuming that growth of whitefish is density dependent, we should detect a decrease in their apparent growth rate following lamprey control. In the North Channel, growth rates changed only slightly during the posttreatment period, but whitefish were consistently larger at all ages than in Georgian Bay or the main basin of Lake Huron (Fig. 5). The faster growth may reflect the fact that North Channel waters are more eutrophic than those of the other areas (Berst and Spangler 1973). The whitefish were possibly growing at a rate close to their maximum potential during the pretreatment period.

Main basin whitefish from the Burnt Island area also have changed little and show a growth rate similar to that of 4–6-yr-old fish from Georgian Bay in the posttreatment period. The growth of Georgian Bay whitefish increased in the posttreatment period. However, the pretreatment era was represented by samples taken from 1956 to 1964 which represented fish whose growth was depressed by the enormous 1943 year-class (Cucin and Regier 1966). This is evident in the continuous progression in growth rate for each year-class up to the control period (data not shown).

Conclusions

Our expectations regarding the response of whitefish populations to lamprey control were partially realized in the North Channel and northern Lake Huron populations where lamprey predation was most severe. As postulated, survival rates of whitefish increased significantly during the lamprey control period. The abundance of lamprey as indicated by the incidence of wounding on whitefish, and the size of assessment barrier catches, also declined during this period but a decline was apparently underway prior to chemical treatment. As expected, whitefish increased in abundance in both areas but an associated decrease in growth rates was not clearly indicated. Only a subtle decrease in size at age was demonstrated by an increase in age at recruitment (to large-mesh gill nets) by one year in the North Channel and a smaller shift in recruitment age in the Lake Huron fishery. We do not expect that additional reductions in lamprey abundance will further enhance survival to a detectable degree. This is certainly the case in the main basin where the intensity of the fishery is sufficient to absorb a slight additional escapement from lamprey predation.

Whitefish population changes in southern Georgian Bay do not reflect a detectable response to reduced lamprey predation, possibly because lamprey induced mortality was not significant there during the study period. Contrary to our expectation, since lamprey control, whitefish abundance has declined and growth rates

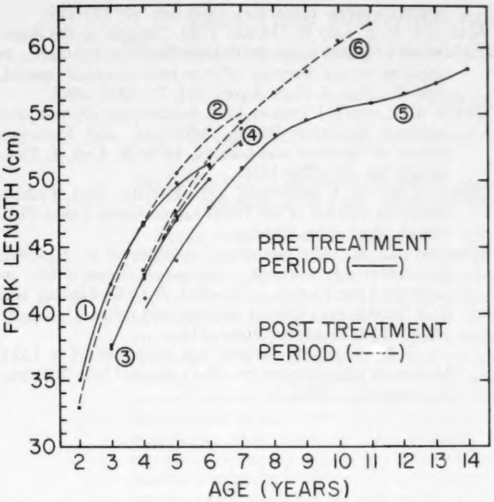

FIG. 5. Mean fork lengths of whitefish taken in 114-mm gill nets during April and May for North Channel (curves 1, in 1958–62 and 2, 1963–75), Burnt Island (curves 3, 1964–71 and 4, 1972–75) and southern Georgian Bay (curves 5, 1956–62 and 6, 1969–74).

have increased considerably, probably as a density-dependent response. Survival rates also declined, primarily because of the extinction of the very large 1943 year-class which dominated the age structure of catches in the 1950s and inflated the survival values in the pretreatment period.

Acknowledgments

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ANON. 1972a. Ontario Commercial fish industry statistics on landings, 1961–1965. Commercial Fish and Fur Branch, Division of Fish and Wildlife, Ontario Ministry of Natural Resources, Toronto, Ont. 55 p.

1972b. Ontario commercial fish industry statistics on landings, 1966–1970. Commercial Fish and Fur Branch, Division of Fish and Wildlife, Ontario Ministry of Natural Resources, Toronto, Ont. 59 p.

APPLEGATE, V. C., J. H. HOWELL, J. W. MOFFETT, B. G. H. JOHNSON, AND M. A. SMITH. 1961. Use of 3-trifluoromethyl-4-nitrophenol as a selective sea lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 1: 35 p.

BERST, A. H., AND G. R. SPANGLER. 1970. Population dynamics of F_1 splake, (*Salvelinus fontinalis* × *S. namaycush*) in Lake Huron. J. Fish. Res. Board Can. 27: 1017–1032.

1973. Lake Huron, the ecology of the fish community and man's effects on it. Great Lakes Fish. Comm. Tech. Rep. 21: 41 p.

BERST, A. H., AND A. A. WAINIO. 1967. Lamprey parasitism of rainbow trout in Southern Georgian Bay. J. Fish. Res. Board Can. 24: 2539–2548.

BUDD, J. C., AND F. E. J. FRY. 1960. Further observations on the survival of yearling lake trout planted in South Bay, Lake Huron. Can. Fish Cult. 26: 7–13.

CHRISTIE, W. J. 1963. Effects of artificial propagation and the weather on recruitment in the Lake Ontario whitefish fishery. J. Fish. Res. Board Can. 20: 597–646.

COLLINS, J. J. 1964. A preliminary report on experimental gill netting in the North Channel of Lake Huron. Ont. Dep. Lands Forests, Tehkummah, Ont. 18 p. (Mimeo)

1971. Introduction of kokanee salmon (*Oncorhynchus nerka*) into Lake Huron. J. Fish. Res. Board Can. 29: 1857–1871.

1979. Relative efficiency of multifilament and monofilament nylon gill net towards lake whitefish (*Coregonus clupeaformis*) in Lake Huron. J. Fish. Res. Board Can. 36: 1180–1185.

CRAIGIE, D. E. 1971. The geographical distribution and spatial associations of fishes in Georgian Bay, Ontario: 1958–1963. Ph.D. thesis, Univ. Toronto, Toronto, Ont. 104 p.

CUCIN, D., AND H. A. REGIER. 1966. Dynamics and exploitation of lake whitefish in Southern Georgian Bay. J. Fish. Res. Board Can. 23: 221–274.

DAHL, F. H., AND R. B. MCDONALD. 1980. Effects of control of the sea lamprey (*Petromyzon marinus*) on migratory and resident fish populations. Can. J. Fish. Aquat. Sci. 37: 1886–1894.

HALL, A. E. JR., AND O. R. ELLIOTT. 1954. Relationship of length of fish to incidence of sea lamprey scars on white suckers, *Catostomus commersoni*, in Lake Huron. Copeia 1954: 73–74.

HEALEY, M. C. 1975. Dynamics of exploited whitefish populations and their management with special reference to the Northwest Territories. J. Fish. Res. Board Can. 32: 427–448.

1978. The dynamics of exploited lake trout populations and implications for management. J. Wildl. Manage. 42: 307–328.

HEINRICH, J. W., J. G. WEISE, AND B. R. SMITH. 1980. Changes in biological characteristics of the sea lamprey (*Petromyzon marinus*) as related to lamprey abundance, prey abundance, and sea lamprey control. Can. J. Fish. Aquat. Sci. 37: 1861–1871.

JOHNSON, B. G. H. 1969. Some statistics of the population of parasitic-phase sea lampreys in Canadian waters of the Great Lakes. Proc. Conf. Great Lakes Res. 12: 45–52.

JOHNSON, B. G. H., AND W. C. ANDERSON. 1980. Predatory-phase sea lampreys (*Petromyzon marinus*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37: 2007–2020.

KING, E. L. JR. 1980. Classification of sea lamprey (*Petromyzon marinus*) attack marks on Great Lakes lake trout (*Sal-*

velinus namaycush). Can. J. Fish. Aquat. Sci. 37: 1989–2006.

LENNON, R. E. 1954. Feeding mechanism of the sea lamprey and its effect on host fishes. U.S. Fish. Wildl. Serv. Fish. Bull. 98: 247–293.

MAITLAND, P. S. 1980. Scarring of whitefish (*Coregonus lavaretus*) by European river lamprey (*Lampetra fluviatilis*) in Loch Lomond, Scotland. Can. J. Fish. Aquat. Sci. 37: 1981–1988.

PARKER, P. S., AND R. E. LENNON. 1956. Biology of the sea lamprey in its parasitic phase. U.S. Fish Wildl. Serv. Res. Rep. 44: 32 p.

REGIER, H. A., AND K. H. LOFTUS. 1972. Effects of fisheries exploitation on salmonid communities in oligotrophic lakes. J. Fish. Res. Board Can. 29: 959–968.

RIDGLEY, J. I. 1976. Ontario commercial fish industry statistics on landings, 1971–1975. Fisheries Branch, Division of Fish and Wildlife, Ontario Ministry of Natural Resources, Toronto, Ont. 55 p.

ROBSON, D. S., AND D. G. CHAPMAN. 1961. Catch curves and mortality rates. Trans. Am. Fish. Soc. 90: 181–189.

SCHULDT, R. J., AND R. GOOLD. 1980. Changes in the distribution of native lampreys in Lake Superior tributaries in response to sea lamprey (*Petromyzon marinus*) control, 1953–77. Can. J. Fish. Aquat. Sci. 37: 1872–1885.

SMITH, B. R., AND J. J TIBBLES. 1980. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936–78. Can. J. Fish. Aquat. Sci. 37: 1780–1801.

SMITH, S. H., H. J. BUETTNER, AND R. HILE. 1961. Fishery statistical districts of the Great Lakes. Great Lakes Fish. Comm. Tech. Rep. 2: 24 p.

SPANGLER, G. R. 1970. Factors of mortality in an exploited population of whitefish, *Coregonus clupeaformis*, in northern Lake Huron, p. 515–529. *In* C. C. Lindsey and C. S. Woods [ed.] Biology of coregonid fishes. University of Manitoba Press, Winnipeg, Man.

1974. Mortality factors and dynamics of a Lake Huron whitefish population. Ph.D. thesis, Univ. Toronto, Toronto, Ont. 130 p.

Lake Trout (*Salvelinus namaycush*) and Sea Lamprey (*Petromyzon marinus*) Populations in Lake Michigan, 1971–78[1,2]

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WELLS, L. 1980. Lake trout (*Salvelinus namaycush*) and sea lamprey (*Petromyzon marinus*) populations in Lake Michigan, 1971–78. Can. J. Fish. Aquat. Sci. 37: 2047–2051.

Lake trout (*Salvelinus namaycush*) was exterminated in Lake Michigan by the mid-1950s as a result of the combined effects of an intensive fishery and predation by the sea lamprey (*Petromyzon marinus*). The widespread application of lampricide in tributary streams had greatly reduced the abundance of lampreys by the early 1960s, and a program to restore self-sustaining populations of lake trout through stocking of yearlings and fingerlings was initiated in 1965. Although the hatchery-reared fish spawned widely in Lake Michigan each year after 1970, no progeny were observed except in an isolated area in Grand Traverse Bay. During 1971–78, sea lamprey abundance was generally greater in Wisconsin than in other parts of the lake. However, the rate of occurrence of sea lamprey wounds on lake trout dropped dramatically there in 1978 after the Peshtigo River, a tributary to Green Bay, was treated with lampricide. Application of Lake Michigan wounding rates to a regression model relating mortality to lamprey wounding developed from Lake Superior data, yielded lamprey-induced mortality estimates in 1977 of 5% in Michigan plus Indiana (combined) and 31% in Wisconsin; corresponding estimates for 1978 were 5 and 15%.

Key words: lake trout, sea lamprey predation, abundance, Lake Michigan

WELLS, L. 1980. Lake trout (*Salvelinus namaycush*) and sea lamprey (*Petromyzon marinus*) populations in Lake Michigan, 1971–78. Can. J. Fish. Aquat. Sci. 37: 2047–2051.

Vers le milieu des années 1950, le touladi (*Salvelinus namaycush*) avait disparu du lac Michigan sous les effets combinés d'une pêche intensive et de la prédation par la grande lamproie marine (*Petromyzon marinus*). Dès le début des années 1960, l'application d'un lampricide dans les tributaires avait considérablement réduit l'abondance des lamproies, et l'on commençait en 1965 un programme visant à rétablir des populations autonomes de touladis au moyen de peuplements de poissons de l'année et de fingerlings. Bien que les touladis de pisciculture aient frayé largement dans le lac Michigan chaque année après 1970, aucune progéniture n'a été observée sauf dans une région isolée de la baie de la Grande Traverse. Pendant la période 1971–78, les lamproies étaient généralement plus abondantes dans le Wisconsin que dans les autres parties du lac. Cependant, le taux d'incidence des blessures résultant d'attaques de lamproies sur le touladi diminua de façon dramatique dans cette région en 1978, une fois la rivière Peshtigo, tributaire de la baie Verte, traitée au lampricide. Quand on applique les taux de blessures du lac Michigan à une modèle de régression reliant la mortalité aux blessures causées par la lamproie, établie à partir de données du lac Supérieur, on obtient des estimations de mortalité causée par la lamproie en 1977 qui sont de 5% au Michigan et dans l'Indiana (combinés) et de 31% dans le Wisconsin; les estimations correspondantes pour 1978 sont de 5% et 15%.

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THE appearance and proliferation of the sea lamprey (*Petromyzon marinus*) in Lake Michigan, and the effects of this parasite on lake trout (*Salvelinus namaycush*) populations, have been described in a sizable body of published and unpublished reports. The most recent published document that dealt with the subject in detail (Wells and McLain 1973) described events through 1970. The primary purpose of the present report is to discuss developments in 1971–78 relative to lake trout and sea lamprey populations in Lake Michigan proper — i.e. the lake exclusive of Green Bay.

Historical Perspective

Lake trout was the most valuable commercial species

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[1] This paper forms part of the Proceedings of the Sea Lamprey International Symposium (SLIS) convened at Northern Michigan University, Marquette, Michigan, July 30–August 8, 1979.

[2] Contribution no. 557 of the Great Lakes Fishery Laboratory, U.S. Fish and Wildlife Service, Ann Arbor, MI 48105, USA.

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in Lake Michigan from 1890 to the mid-1940s (Wells and McLain 1973). Production during that period was usually higher in Lake Michigan than in any of the other Great Lakes. The annual catch in millions of kilograms averaged 3.7 in 1890–1911, declined to 3.2 in 1912–26, dropped further to 2.4 in 1927–39, and then (largely resulting from increased fishing intensity) increased to 3.3 in 1940–44. A precipitous decline that began in 1945 led to a catch of only 155 000 kg in 1949. By 1956 the species evidently had become extinct in Lake Michigan.

Sea lamprey was first reported in Lake Michigan in 1936 (Applegate 1950). It proliferated rapidly, and by the early 1940s fishermen were complaining of high incidences of lamprey wounds on fish in their catches (Shetter 1949). Lake trout was the primary victim, although other species were also severely attacked. Few biologists doubt that sea lamprey predation was a leading cause of the decline and extermination of lake trout in the 1940s and early 1950s. Hile et al. (1951) and Eschmeyer (1957) believed that lamprey was totally at fault. Smith (1968), however, speculated that although the sea lamprey hastened the decline once it had begun, the downward trend was initiated by extremely heavy fishing in 1940–44. Wells and McLain (1973) held the lamprey primarily responsible, although they believed the lake trout stocks were being somewhat overexploited even before the parasite entered the lake.

Sea lamprey control began in 1953. Early efforts with electrical (and a few mechanical) barriers gave way in 1960 to more effective chemical control with a selective toxicant applied to lamprey larvae in nursery streams. The success of the chemical control was shown by declines in numbers of spawning-run sea lampreys caught at three barriers that were left in operation to provide yearly indices of lamprey abundance. Catches dropped from 12 886 in 1961 to 1168 in 1966 (after which the barriers were removed because of budgetary limitations).

A program to restore self-sustaining populations of lake trout in Lake Michigan, coordinated by the Great Lakes Fishery Commission (GLFC), was initiated in 1965. An average of about 2.2 million lake trout were released into the lake annually in 1965–78. Most were stocked in spring as yearlings, but some were planted in fall as fingerlings.

Materials and Methods

Data on the biology and abundance of lake trout, and population trends of sea lampreys, came from experimental gillnet collections made by the U.S. Fish and Wildlife Service and by the states bordering Lake Michigan — Wisconsin, Michigan, Indiana, and Illinois. Collections of lake trout data beginning in 1976, and sea lamprey data beginning in 1971, were made through a lakewide interagency effort coordinated by the GLFC. To assess lake trout stocks, each agency systematically fished standard graded-mesh gill nets (30 m each of eight meshes [cm, stretched measure]: 6.4, 7.6, 8.9, 10.2, 11.4, 12.7, 14.0, and 15.2) at several depths within the primary depth range occupied by trout at the time of sampling. Most sampling was conducted between June and September. Trends in sea lamprey abundance were derived from fall surveys of wounding rates on lake trout. Each year the survey data from all agencies were combined into a single report to GLFC, in which rates were customarily presented separately for four regions of the lake: Wisconsin; northern Michigan (Michigan Fishery Statistical Districts 1–5); southern Michigan–Indiana; and Illinois (Fig. 1). Data for each region came from one to four sampling sites, which changed in location somewhat from year to year and usually totaled about 10 for the entire lake. To estimate lamprey-induced mortaltiy in lake trout, I used Pycha's (1980) regression model.

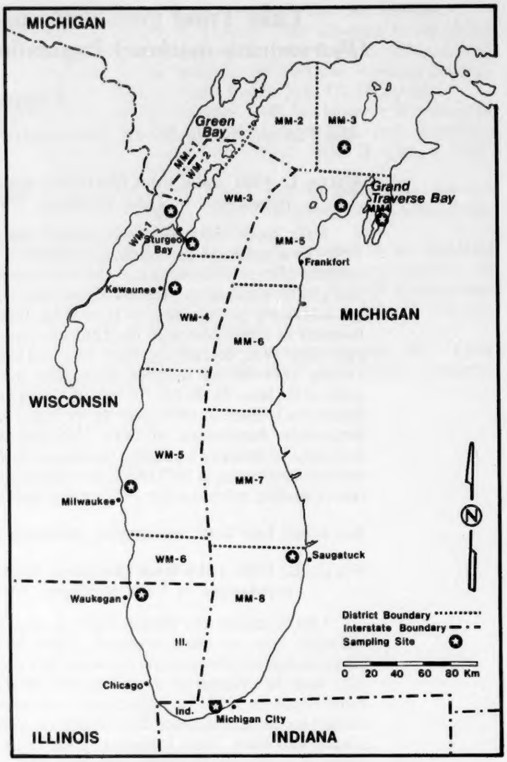

FIG. 1. Lake Michigan, showing interstate boundaries, statistical districts, and sites sampled for sea lamprey wounding data in 1977 and 1978.

Status of Lake Trout and Sea Lampreys

LAKE TROUT

Lake trout stocked in Lake Michigan grew rapidly, attaining an average length of about 50 cm after completion of 4 yr of life. The average length of native

Lake Michigan lake trout of the same age was only 34 cm during 1947–51 (Eschmeyer 1957). Most of the stocked fish became mature at age VI, although a few males matured at age V.

The lake trout restoration program succeeded in establishing a conspicuous spawning population in Lake Michigan, although some biologists question whether the numbers of spawners approached those of the prelamprey period. Rybicki and Keller (1978), basing their computations on data collected by the Michigan Department of Natural Resources (MDNR), estimated that in 1975, Michigan Statistical Districts 4–8 (Fig. 1) contained 93 000 lake trout of age VI and older (maximum age X). Extrapolated to the entire lake (including Green Bay), the value would approximate 244 000. R. W. Hatch (Great Lakes Fishery Laboratory, Ann Arbor, Michigan, personal communication), using data collected by the MDNR and the U.S. Fish and Wildlife Service, estimated the population of age VI and older lake trout in all of State of Michigan waters in 1978 as 203 000, which extrapolates to about 347 000 for the entire lake. Much of the increase from 1975 to 1978 resulted from higher stocking rates that began in 1971.

Commercial fishing for lake trout in Lake Michigan was prohibited throughout 1971–78, but anglers took considerable numbers each year. According to estimates by the respective state agencies, the sport catch in 1978 was 106 000 in Michigan, 61 000 in Wisconsin, and 2000 in Indiana (no estimates for Illinois).

Although the hatchery-reared lake trout spawned widely in Lake Michigan each year after 1970, no young were produced, at least in detectable numbers, except in one small area of Grand Traverse Bay. There, lake trout are known to have hatched in 1977 and 1978 from eggs deposited among rocks placed around the cooling-water intake of a power plant. The fate of the hatched fish is not known, however, except that some survived to a length of at least 36 mm (T. M. Stauffer, MDNR, Marquette, Michigan, personal communication). Several hypotheses have been advanced to explain the near-failure of the hatchery fish to produce progeny. Biologists have theorized, for example, that the hatchery fish failed to spawn in suitable areas; that the stocked fish were somehow genetically unsuited to reproducing successfully in Lake Michigan; that pollutants destroyed eggs or fry directly, or caused degradation of spawning substrate; and that predators took a major share of the eggs or fry. One view that gained considerable support was that the spawning population was simply too small to have much chance of producing significant numbers of progeny, considering the extremely high mortality to be expected among eggs and fry of fish that are poorly adapted to reproducing in the lake.

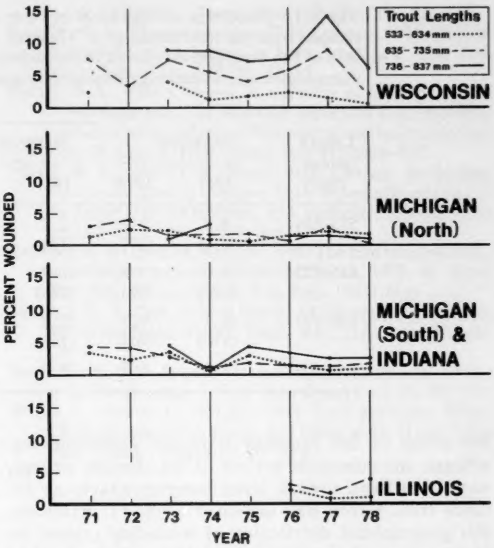

FIG. 2. Sea lamprey wounding rates (%) on lake trout of three length groups, in different regions of Lake Michigan, fall 1971–78. Individual data points are based on samples of 58–2295 fish (average 465).

SEA LAMPREYS

Sea lamprey wounding rates on lake trout in the falls of 1971–78 were generally higher in Wisconsin than in the other parts of the lake (Fig. 2). Rates in Wisconsin (%) ranged from 0.3 to 2.5 (average 1.7) for fish 533–634 mm long; 2.2 to 8.1 (average 5.3) for fish 635–735 mm long; and 5.6 to 13.2 (average 7.9) for fish 736–837 mm long. In contrast, rates among fish in the successively larger size-categories fluctuated little around averages of 1.0, 1.4, and 1.6 in waters of northern Michigan, and 1.6, 1.9, and 2.4 in southern Michigan–Indiana. Rates in Illinois during 1976–78 (based on generally scanty data) averaged 0.7 and 2.5% for the smallest and intermediate size-categories, respectively (no data for largest category). Chi-square tests on the combined data for all years showed that the wounding rates for each of the two largest size-groups of fish were significantly greater ($P < 0.01$) in Wisconsin than in either northern Michigan or southern Michigan–Indiana.

A pronounced reduction in wounding in Wisconsin between 1977 and 1978 merits special comment. A clearer understanding of events is provided by separate examination of the 1977 and 1978 data from the four sites in Wisconsin — one in Green Bay, and three in the lake proper — at which samples were obtained in those years (Table 1). In 1977, wounding rates for each of the size-categories of lake trout were highest in Green Bay and successively lower at Sturgeon Bay, Kewaunee, and Milwaukee. Although the individual differences from one locality to the next for a given

TABLE 1. Percentage of lake trout of three size-groups bearing sea lamprey wounds in fall samples from different localities in Wisconsin waters of Lake Michigan, 1977 and 1978 (Numbers of fish examined are shown in parentheses).

Length group (mm)	Green Bay		Lake proper					
			Sturgeon Bay		Kewaunee		Milwaukee	
	1977	1978	1977	1978	1977	1978	1977	1978
533–634	6.5 (31)	0.0 (39)	2.2 (178)	0.8 (119)	0.9 (110)	0.0 (96)	0.0 (118)	0.0 (124)
635–735	18.0 (128)	2.9 (68)	10.7 (224)	4.3 (257)	5.1 (297)	2.6 (189)	1.4 (139)	0.3 (359)
736–837	19.1 (136)	9.7 (62)	12.8 (149)	8.0 (137)	10.7 (169)	9.6 (187)	8.3 (60)	0.7 (271)
Average	14.5	4.2	8.6	4.3	5.6	4.1	3.2	0.3

size-group of fish generally were not statistically significant, the consistent pattern of the changes strongly suggests a trend toward fewer lamprey attacks as distance from Green Bay increased (Fig. 1). Evidently, this geographical distribution of wounding existed because many of the marks on lake trout in the lake proper, particularly on fish nearest to Green Bay, were made by lampreys that had migrated from the bay. Evidence for this conclusion is provided by the drops observed in wounding rates at all sampling sites in 1978 (Table 1), following treatment with lampricide in 1977 of the Peshtigo River, a Green Bay tributary that became heavily infested with sea lamprey ammocoetes when pollution control efforts improved its water quality. As might be expected, the declines were particularly pronounced in Green Bay and at Sturgeon Bay.

Effects of Sea Lampreys on Lake Trout

Data are not available for a detailed quantitative analysis of the effects of sea lampreys on lake trout in Lake Michigan proper. Relating changes in abundance of lampreys to changes in either abundance or mortality of lake trout is not possible, because lamprey populations do not seem to have changed materially in most of the lake. Where significant changes have occurred, data on lake trout populations are inadequate for attempting to establish the relation. Perhaps an indication of the general magnitude of lamprey-induced mortality in Lake Michigan can be gained by applying wounding rates in Lake Michigan to Pycha's (1980) regression model, in which he showed a curvilinear relation between spring wounding rates and total natural mortality of lake trout in Lake Superior.

To apply Lake Michigan wounding rates, which are collected in fall, to Pycha's model, I derived a factor to convert fall to spring rates. I considered this procedure necessary because Pycha and King (1975) showed that wounding rates in Lake Superior varied appreciably with time of year. The computation had to be based on a single set of data. The data were collected by the Wisconsin Department of Natural Resources off Sturgeon Bay in September–October 1975 and April 1976 (wounds in the two periods were produced by the same generation of lampreys, except that in spring a few newly transformed individuals might have been involved). Wounding rates and sample sizes (in parentheses) for the different length groups of lake trout in the two periods were as follows:

Length group (mm)	Sept.–Oct.	April
533–634	2.4 (126)	2.7 (184)
635–735	4.0 (730)	12.0 (167)
736–837	6.4 (498)	11.2 (125)
Unweighted average	4.3	8.6

The average of the percentages for the three sizes of fish was twice as great in the spring (8.6) as in the previous fall. Accordingly, I have used a factor of 2 in converting from fall to spring rates — recognizing the limitations of the data from which the figure was derived.

I have combined the wounding data for northern Michigan and southern Michigan–Indiana (since the rates were similar in these two areas) and computed the lamprey-induced mortality separately for Michigan–Indiana and Wisconsin, for 1977 and 1978.

The average fall wounding rate of the three size-groups of lake trout in Michigan–Indiana in 1977 was 1.1%, which converts to a spring rate of 2.2%. Applied to Pycha's model, this wounding rate corresponds to an instantaneous total mortality of 0.31. Since the model yielded an estimate for instantaneous nonlamprey-induced natural mortality of 0.26 (assumed to be constant), the total mortality value corresponds to an instantaneous lamprey-induced mortality of 0.05 (0.31

-0.26), or a conditional annual lamprey-induced mortality of 5%. Similarly, a fall wounding rate of 1.0% in 1978 also corresponds to an annual lamprey-induced mortality of 5%. (The estimated total instantaneous natural mortality for both years, 0.31, is closely similar to Rybicki and Keller's [1978] estimate of 0.28 for State of Michigan Statistical Districts 3–8 in 1975). Computed by the same method, the annual lamprey-induced mortality in Wisconsin waters was much higher at 31% in 1977 and 15% in 1978. These percentages, though admittedly rough approximations, suggest that although sea lamprey predation during 1971–78 may not have contributed greatly to lake trout mortality in Michigan–Indiana, it was a major source of mortality in Wisconsin.

APPLEGATE, V. C. 1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 55: 237 p.

ESCHMEYER, P. H. 1957. The near extinction of the lake trout in Lake Michigan. Trans. Am. Fish. Soc. 85: 102–119.

HILE, R., P. H. ESCHMEYER, AND G. F. LUNGER. 1951. Decline of the lake trout fishery in Lake Michigan. U.S. Fish Wildl. Serv. Fish. Bull. 52: 77–95.

PYCHA, R. L. 1980. Changes in mortality of lake trout (*Salvelinus namaycush*) in Michigan waters of Lake Superior in relation to sea lamprey (*Petromyzon marinus*) predation, 1968–78. Can. J. Fish. Aquat. Sci. 37: 2063–2073.

PYCHA, R. L., AND G. R. KING. 1975. Changes in the lake trout population of southern Lake Superior in relation to the fishery, the sea lamprey, and stocking, 1950–70. Great Lakes Fish. Comm. Tech. Rep. 28: 33 p.

RYBICKI, R. W., AND M. KELLER. 1978. The lake trout resource in Michigan waters of Lake Michigan, 1970–76. Mich. Dep. Nat. Resourc. Fish. Res. Rep. 1863: 71 p.

SHETTER, D. S. 1949. A brief history of the sea lamprey problem in Michigan waters. Trans. Am. Fish. Soc. 76: 160–176.

SMITH, S. H. 1968. Species succession and fishery exploitation in the Great Lakes. J. Fish. Res. Board Can. 25: 667–693.

WELLS, L., AND A. L. MCLAIN. 1973. Lake Michigan: Man's effects on native fish stocks and other biota. Great Lakes Fish. Comm. Tech. Rep. 20: 55 p.

Changes in Mortality of Lake Trout (*Salvelinus namaycush*) in Relation to Increased Sea Lamprey (*Petromyzon marinus*) Abundance in Green Bay, 1974–78[1]

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MOORE, J. D., AND T. J. LYCHWICK. 1980. Changes in mortality of lake trout (*Salvelinus namaycush*) in relation to increased sea lamprey (*Petromyzon marinus*) abundance in Green Bay, 1974–78. Can. J. Fish. Aquat. Sci. 37: 2052–2056.

Increased sea lamprey (*Petromyzon marinus*) abundance in Green Bay during 1977 is documented utilizing sea lamprey counts and lake trout (*Salvelinus namaycush*) wounding as methods of measurement. Since lake trout rehabilitation began in 1965, sea lamprey predation has been consistently higher in Green Bay and Northern Lake Michigan than other areas of the lake. It appears that increased sea lamprey predation in Green Bay, above the former high levels, resulted in decreased abundance and increased mortality of lake trout. The increase in lampreys is related to the colonization of the Peshtigo River, Marinette County, Wisconsin.

Key words: Green Bay, sea lamprey increases, Peshtigo River, lake trout, increased mortality

MOORE, J. D., AND T. J. LYCHWICK. 1980. Changes in mortality of lake trout (*Salvelinus namaycush*) in relation to increased sea lamprey (*Petromyzon marinus*) abundance in Green Bay, 1974–78. Can. J. Fish. Aquat. Sci. 37: 2052–2056.

L'abondance accrue de la grande lamproie marine (*Petromyzon marinus*) dans la baie Verte en 1977 est démontrée à l'aide de dénombrements de lamproies et d'incidence de blessures sur le touladi (*Salvelinus namaycush*). Depuis le début de la réhabilitation du touladi en 1965, la prédation par la grande lamproie marine a été uniformément plus élevée dans la baie Verte et dans le nord du lac Michigan que dans les autres régions du lac. Il semble que la prédation accrue par la lamproie dans la baie Verte, dépassant les hauts hiveaux antérieurs, ait causé une diminution d'abondance et une augmentation de mortalité des touladis. L'abondance accrue de la lamproie est liée à la colonisation de la rivière Peshtigo, dans le comté de Marinette, au Wisconsin.

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HISTORICALLY lake trout (*Salvelinus namaycush*) have been an important species in the commercial fishery of Green Bay. Although production records for the Bay were not kept separate from those of Lake Michigan until 1953, it is known that ports located on the northwest side of Door County, Wisconsin, once ranked as major producers of lake trout. Other Green Bay ports along the western shore were also major contributors. The disappearance of lake trout stocks in Lake Michigan and Green Bay by the early 1950s has been blamed on the invasion of the sea lamprey (*Petromyzon marinus*), which also threatened species such as the lake whitefish (*Coregonus clupeaformis*) and burbot (*Lota lota*) (Eschmeyer 1957; Hile et al. 1951; Wells and McLain 1972).

Sea lamprey control made feasible the stocking of lake trout in an attempt to rehabilitate this species in 1965. In 1965–78, 2.3 million yearling lake trout were stocked into Wisconsin's waters of Green Bay (Table 1), of which two-thirds were stocked northwest of Sturgeon Bay, in grid 804 (Fig. 1).

Sea lamprey predation has been detrimental to lake trout rehabilitation efforts in Green Bay perhaps to a greater extent than any other area of Lake Michigan. After lake trout restocking began, sea lamprey predation, indicated by wounds and scars on lake trout, was not an apparent problem until lake trout reached larger sizes in 1968 and 1969. Since then, wounding rates on lake trout from Michigan and Wisconsin waters of Green Bay have been the highest observed in Lake Michigan during the last 11 yr (Great Lakes Fishery Comm. 1969–79). Tributary streams along the western shore of Green Bay and northern Lake Michigan have been major producers of sea lampreys. Some streams because of industrial and municipal pollution, were not sea lamprey producers during the 1950s and 1960s;

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[1] This paper forms part of the Proceedings of the Sea Lamprey International Symposium (SLIS) convened at Northern Michigan University, Marquette, Michigan, July 30–August 8, 1979.

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TABLE 1. Lake trout stocked in Wisconsin waters of Green Bay, 1965–78.

Year	Grid no.	Thousands of lake trout	Stocking site/Method
1965	606	105	Gills Rock (Shore)
1966	804	190	Green Bay (Ferry)
1968	606	185	Gills Rock (Ferry)
	605	193	Green Bay (Ferry)
1969	804	100	Green Bay (Ferry)
1970	804	200	Stone Quarry (Shore)
1971	804	221	Stone Quarry (Shore)
1972	804	132	Stone Quarry (Shore)
1973	804	110	Stone Quarry (Shore)
1974	606	25	Gills Rock (Shore)
	804	93	Stone Quarry (Shore)
1975	505	35	Whaleback Shoal (Ferry)
	606	37	Death Door Bluff (Ferry)
	804	48	Larson's Reef (Shore)
	804	100	Larson's Reef (Shore)
1976	606	70	Horseshoe Reef (Ferry)
	804	102	Larson's Reef (Shore)
1977	804	45	Larson's Reef (Shore)
	804	55	Larson's Reef (Shore)
	606	53	Death Door Bluff (Ferry)
1978	606	65	Horseshoe Reef (Ferry)
	804	141	Larson's Reef (Shore)

however, sea lamprey surveys conducted by U.S. Fish and Wildlife Service (USFWS) have shown that many of these streams must now be treated because of the success of pollution abatement efforts.

Since 1974, the Wisconsin Department of Natural Resources (WDNR) has routinely sampled the area known as Larson's Reef in grid 804 (Fig. 1), as well as other areas in Lake Michigan, primarily to collect lake trout wounding and scarring data; however, changes in catch per effort (CPE) has also provided a measurement of abundance. Examination of fin clips from lake trout samples collected from Green Bay, WM-1 and WM-2, and from Lake Michigan, WM-3 and WM-4 (Fig. 1), indicate no major movement of lake trout from Green Bay (WDNR unpublished data). Furthermore, no evidence of natural reproduction of lake trout has been found to date.

The purpose of this paper is to relate the apparent increase in sea lamprey abundance, as measured by the USFWS surveys, and increased wounding rates documented by the WDNR, to the decrease in lake trout abundance (as reflected by CPE) and associated increases in mortality.

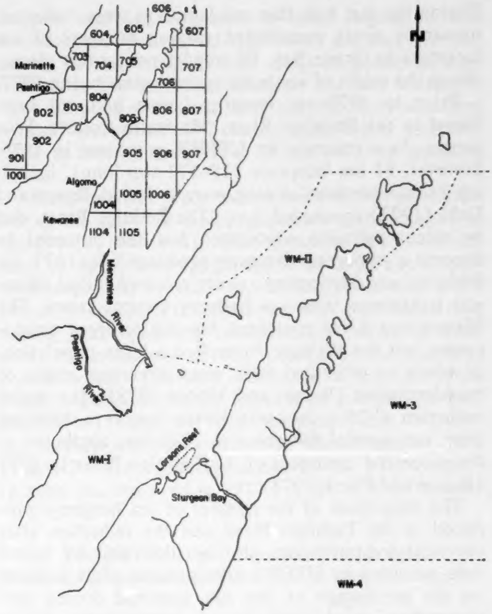


FIG. 1. Green Bay showing statistical district's WM-1 and WM-2, Larson's Reef, and the Peshtigo and Menominee rivers. Lake Michigan statistical districts WM-3 and WM-4 and smaller grid areas (numbered areas) are also shown.

Sea Lamprey Abundance

Sea lamprey abundance in Lake Michigan and Green Bay has been directly monitored by the USFWS utilizing sea lamprey pretreatment surveys, trapping adults during spawning runs, and collections of parasitic phase sea lampreys from commercial fishermen. Additionally, the WDNR has monitored wounding rates on lake trout which indirectly measures changes in abundance of parasitic phase sea lampreys. Increases in sea lamprey abundance in Green Bay during 1977, measured by these methods, appears to be related to the establishment of a sea lamprey population in the Peshtigo River.

DIRECT MEASURES

Since 1971, the USFWS has assessed the abundance of parasitic phase sea lampreys through the collection of lampreys captured by commercial fishermen during their netting operations. William C. Anderson (USFWS Marquette, Michigan) who has collected most of the lampreys from the fishermen, provided the following information on numbers collected from Green Bay:

Year	No. of sea lamprey collected
1971	697
1972	699
1973	507
1974	461
1975	291
1976	288
1977	1110
1978	89

During the last 8 yr that sea lampreys were collected, numerous rivers contributed varying numbers of sea lampreys to Green Bay. Of importance in this discussion is the origin of sea lampreys collected during 1977.

Prior to 1976 sea lamprey larvae had not been found in the Peshtigo River, Marinette County, Wisconsin. In a resurvey by USFWS personnel in 1976, however, 91 sea lampreys (28–173 mm long), including 7 that were transforming, were collected. Braem and Dahl (1977) concluded that, "The Peshtigo River, due to recent pollution abatement, has the potential to become a major sea lamprey producer." In 1977 the Peshtigo and Menominee rivers received initial chemical treatments from sea lamprey control crews. The Menominee River contained few sea lamprey ammocoetes, but the Peshtigo River had a large population, of which an estimated 60% were in various stages of transformation (Braem and Moore 1978). The major reduction (92%) in parasitic sea lampreys collected from commercial fishermen in 1978 was attributed to the successful treatment of the Peshtigo River in 1977 (Braem and Purvis 1978).

The magnitude of the number of sea lampreys produced in the Peshtigo River and the reduction after chemical treatment can also be illustrated by recent data provided by USFWS (the percent effort is based on the percentage of the run captured during corresponding dates and water temperatures where USFWS personnel felt information was complete):

River and year	Dates in operation	Total catch	% effort
Peshtigo			
1977	Apr. 20–May 20	644	47
1978	Apr. 18–June 9	2360	100
1979	Apr. 17–June 17	264	100
Menominee			
1977	May 10–May 20	714	39
1978	Apr. 20–June 9	1827	100
1979	May 5–June 17	131	96

Evidence collected by sea lamprey control staff of the USFWS documents a decline in sea lamprey abundance in Green Bay during the early 1970s and a sharp increase in 1977. A year later, increased abundance also occurred in the spawning runs to the Peshtigo and Menominee rivers. This increase appears to reflect colonization of the Peshtigo River about 1972 after water quality in that river improved greatly as a consequence of effective removal of pulp mill and paper mill discharges to the stream. Further improvement occurred in 1974 by treatment of all discharges in a new municipal sewage treatment plant (WDNR Water Quality Section personal communication).

INDIRECT MEASURES

Each fall from 1974 to 1978 data were collected by the WDNR research vessel *Barney Devine* on lake trout at Larson's Reef (Fig. 1). Graded-mesh gill nets by 13-mm increments from 64 to 152 mm (stretch measure) were fished. Each lake trout captured was measured, examined for fin clips and for evidence of sea lamprey wounding.

TABLE 2. Lake trout lamprey wounding grid 804, 1974–78.

Length of lake trout and year	Sample size	% wounded
634–735 mm		
1974	432	5.8
1975	317	3.8
1976	639	6.3
1977	128	18.0
1978	68	2.9
736–837 mm		
1974	217	7.4
1975	225	7.6
1976	277	6.9
1977	136	19.1
1978	62	9.7

Sea lamprey wounding data indicate increases in wounding rates in 1977 on all size ranges of lake trout 533 mm and greater in length. Substantial increases occurred on the most thoroughly sampled size ranges (Table 2). Lake trout 634–735 mm in length showed an increase in wounding rates from 6.3% in 1976 to 18.0% in 1977. A similar increase in wounding on the 736–837 mm size range occurred between 1976 and 1977; wounding increased 12.2 percentage points in 1977 to a rate of 19.1%.

Lake Trout Abundance

During the years of sampling by WDNR each lake trout caught on Larson's Reef was assigned an age based on fin clip identification. Sampling was conducted during the fall spawning period; therefore, representative numbers of fish within age-groups begin at age 6, the approximate age of maturation. Since fishing effort at Larson's Reef ranged from 4389 m of gill net in 1976 to 10 241 m in 1978, the age distribution of lake trout for each sampling year is given in terms of CPE (Table 3). The CPEs of fish from all age-groups decreased significantly during 1977 and 1978 as compared with the numbers in 1976.

Changes in Lake Trout Mortality

The apparent decline in lake trout abundance (based on CPEs) as well as the increase in wounding rates and increase in lamprey abundance in 1977 prompted investigation into changes in lake trout mortality. Catch curves were derived from CPE data and estimates of total annual mortality were made (Fig. 2). Annual mortality rates ranged from a maximum of 0.65 in 1974 to a minimum of 0.52 in 1975 during the period 1974–76. The annual mortality rates for the 1977 and

TABLE 3. Lake trout age distribution by CPE[a] (ages 6–12) Larson's Reef WM-1, 1974–78.

	Age							
Year	6	7	8	9	10	11	12	N[b]
1974	64.7	16.3	5.1	7.3	0.5			693
1975	23.9	27.8	9.3	2.4	2.3	0.9		610
1976	36.0	35.7	27.2	7.9	1.6	1.4		1010
1977	3.4	3.1	6.4	3.4	1.5	1.2	0.2	297
1978	3.1	0.9	1.2	1.2	0.9	0.5		164

[a] Number of lake trout/304.8 m of gill net.

[b] Sample size represents the total of all fish aged by use of assigned fin clips including ages 1–5.

1978 sampling years appear to decrease. However, this reduction cannot be reconciled with the fact that the total abundance of lake trout decreased, exemplified specifically by the decreasing CPE.

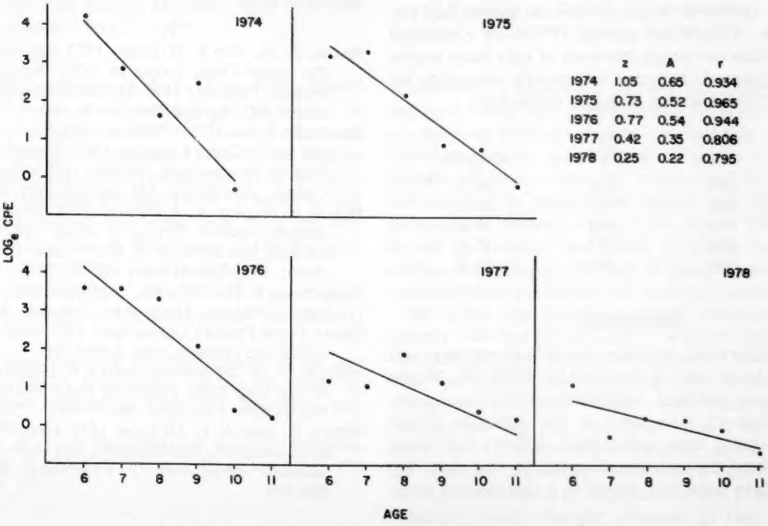
The low mortality rate associated with samples taken in 1977 and 1978, 0.35 and 0.22, respectively, do not appear to be realistic or meaningful. The cause of this decrease in total annual mortality rate is not clear, but indications are that differential rates of mortality were occurring on the various age-groups and associated size ranges of fish. In this case, mortality may have affected the younger age-groups to a greater degree than the older groups, and therefore, given the appearance of decreasing total annual mortality.

Each year-class of parasitic lamprey recruits to Green Bay partly in late fall and through the winter, but mostly during the following spring. They contribute to the mortality experienced by lake trout through the summer and fall but, also to some degree, several months after the annual lake trout samples are collected. In this manner, each lamprey year-class contributes to the mortality estimates for two successive trout sampling years, and therefore, the more abundant lamprey recruits of 1977 should cause higher mortality rates on trout in both 1976/77 and 1977/78 sampling years.

Mortality rates were calculated within year-classes during the 1974–78 sampling periods and arranged by age-groups (Table 4). The extremely low mortality rates on the various age-groups in 1975/76 can be partially explained by restricted fishing effort over a 3-d period. In so doing, the effort may have been fished only during peak spawning concentrations while in other years the effort was spread throughout the spawning period which effectively decreased CPEs. However, Table 4 still confirms the increase in mortality in both the 1976/77 and 1977/78 sampling years. Furthermore, they correlate well with the wounding data (Table 2); the wounding caused by the 1977 lamprey recruits was observed in 1977 but not in 1978 because

TABLE 4. Total annual mortality (A) at ages.

	Ages		
Years	7–8	8–9	9–10
1974/75	0.43	0.53	0.68
1975/76	0.02	0.16	0.36
1976/77	0.82	0.88	0.82
1977/78	0.60	0.82	0.73



	z	A	r
1974	1.05	0.65	0.934
1975	0.73	0.52	0.965
1976	0.77	0.54	0.944
1977	0.42	0.35	0.806
1978	0.25	0.22	0.795

FIG. 2. Catch curves for 1974–78 data, ages 6 and older.

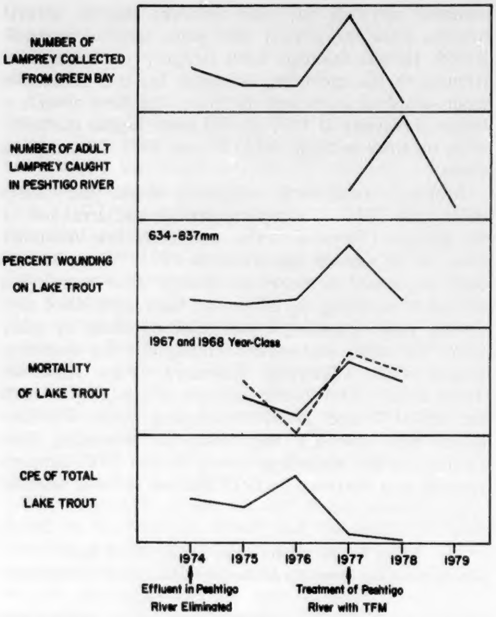


FIG. 3. Relative changes in the parameters measured during the period 1974–78. (Broken line represents the 1968 year-class.)

in 1978 the lake trout were not sampled until well after predation by that year-class had occurred and the lamprey had spawned. It can further be shown that the mean lengths of these age-groups (1974–78 combined data) fall within the length intervals of lake trout which showed the greatest increases in lamprey wounding by comparing Table 2 and 4 with the following:

Age	Sample size	Mean length (mm)	SD (mm)
6	761	696	44.5
7	656	729	34.3
8	443	747	39.6
9	228	777	37.3
10	184	803	38.9

Discussion

Factors other than lamprey predation certainly affected lake trout during the period 1974–78. While sportfishing was minimal, exploitation rates, due to the incidental catch of lake trout in the whitefish gillnet fishery may have been substantial. Efforts had been made to reduce the incidental catch in the past. By 1970, when lake trout had grown to a size making them vulnerable to gill netting, major lake trout stocking in Green Bay was shifted away from the northern area where gillnetting effort was high to grid 804 (Fig. 1). However, while emmigration of trout from Green Bay is minimal, tagging studies have shown widespread movement within the Bay (WDNR Sturgeon Bay unpublished data) making them vulnerable to gillnetting efforts throughout the Bay. During the study period whitefish gillnet effort ranged from 6 231 000–10 705 000 m of gill net in statistical districts WM-1 and WM-2 (Fig. 1), reaching a peak of 10 806 000 m in 1977. Although data are not available to estimate accurately the extent of the incidental catch or the amount of lake trout withdrawn due to illegal fishing operations, this increase in gillnet effort surely affected the total annual mortality of lake trout.

The cause and effect relationships that were addressed in this study are clearly and dramatically summarized in Fig. 3. If the exploitation component of annual mortality was extensive during these years, then the increase in wounding rates may well have been due to a change in the predator–prey relationship. However, it would seem to be more than mere coincidence that extremely high wounding rates (above those in other years) and substantial increases in sea lamprey abundance occurred at a time when lake trout abundance was decreasing. To what extent increases in sea lamprey wounding rates can be used to quantify lamprey induced mortality is impossible without measurement of the other components of mortality. Unmeasured variables makes this discussion documentary rather than analytical, but the Larson's Reef data show explicitly that lake trout rehabilitation efforts can fluctuate from apparent success to near collapse in an extremely short period of time.

BRAEM, R. A., AND F. H. DAHL. 1977. Sea lamprey control in the upper Great Lakes in 1976. Report to lake committees, February 1977. Great Lakes Fish. Comm., Ann Arbor, MI. Agenda Item IV A., 6 p.

BRAEM, R. A., AND H. H. MOORE. 1978. Sea lamprey control in the upper Great Lakes in 1977. Report to Great Lakes Fishery Commission, March 1978. Great Lakes Fish. Comm., Ann Arbor, MI. Agenda Item V A., 7 p.

BRAEM, R. A., AND R. A. PURVIS. 1978. Interim report on sea lamprey control. Report to Great Lakes Fishery Commission, November 1978. Great Lakes Fish. Comm., Ann Arbor, MI, Agenda Item VIII B., 17 p.

ESCHMEYER, P. H. 1957. The near extinction of lake trout in Lake Michigan. Trans. Am. Fish. Soc. 85: 102–119.

GREAT LAKES FISHERY COMMISSION. 1969–1979. Lake Michigan committee minutes. Ann Arbor, MI.

HILE, R., P. H. ESCHMEYER, AND G. F. LUNGER. 1951. Decline of the lake trout fishery in Lake Michigan. U.S. Fish Wildl. Serv. Fish. Bull. 60: 77–95.

WELLS, L., AND A. L. MCLAIN. 1972. Lake Michigan: effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 889–898.

On Evaluating Measures to Rehabilitate Lake Trout (*Salvelinus namaycush*) of Lake Superior[1,2]

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The Lake Superior lake trout (*Salvelinus namaycush*) population is being rebuilt following its collapse in the early 1950s. Estimates are presented of the contributions to this recovery provided directly by the artificial recruitment of hatchery fish, a demonstrable amelioration in mortality rates and a resurgence, lately, of natural recruitment. Of the increased lake trout abundance, 55% on the average was owing to trebling the planting density, 40% to improved survival, and 5% to increasing recruitment of native lake trout. The precise contribution of the sea lamprey (*Petromyzon marinus*) control program could not be defined for lack of sufficient early data.

Key words: lake trout, sea lamprey, rehabilitation, natural recruitment, hatchery stocking

LAWRIE, A. H., AND W. MACCALLUM. 1980. On evaluating measures to rehabilitate lake trout (*Salvelinus namaycush*) of Lake Superior. Can. J. Fish Aquat. Sci. 37: 2057–2062.

Après l'affaissement du début des années 1950, la population de touladis (*Salvelinus namaycush*) du lac Supérieur est en train de se rétablir. Nous présentons des estimations des facteurs qui ont contribué à ce rétablissement, directement par le recrutement artificiel de poissons d'élevage, une amélioration démontrable des taux de mortalité et, dernièrement, le rebondissement du recrutement naturel. Sur l'abondance accrue des touladis, 55% en moyenne est dû au triplement de la densité des peuplements, 40% à une meilleure survie et 5% au recrutement croissant de touladis indigènes. A cause du manque de données suffisantes dans les débuts, il est impossible de définir la contribution précise du programme de contrôle de la grande lamproie marine (*Petromyzon marinus*).

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THE catastrophic collapse in Lake Superior's annual lake trout (*Salvelinus namaycush*) yields which fell at virtually 27% a year from 1953 until 1962 has been documented in considerable detail (Lawrie and Rahrer 1972; Pycha and King 1975; Smith and Tibbles 1980; and others). It need not be elaborated on here, except to note that the decline was coincident with the dispersal and rapid increase in abundance of the sea lamprey (*Petromyzon marinus*) in Lake Superior.

This scenario essentially replicated earlier experience on both Lakes Huron and Michigan and, moreover, occurred at a time when commercial fishing effort also declined so that the circumstantial evidence implicating sea lamprey predation as the culprit was overwhelming. Hence, measures to retrieve the situation centered on a massive effort to reduce the numbers of sea lamprey in the lake and to supplement natural recruitment by the planting of hatchery-reared lake trout. This paper attempts to evaluate the extent to which reduced mortalities and a rapid increase in planting densities have contributed to rebuilding the depleted stocks.

By 1962, the numbers of sea lamprey had been sharply reduced and, by 1975, 40.6 million lake trout had been planted into Lake Superior. The vast majority were spring-planted yearling fish. All of these were finclipped, mostly with double clips. Since there is little likelihood of perfect regeneration of both fins, fish of hatchery origin can be recognized on recapture, and the observed abundance of hatchery-derived lake trout can be related to the magnitude of the plantings which produced them. Secular changes in this relationship provide a basis for evaluating the relative importance of the two rehabilitative measures.

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TABLE 1. Thousands of finclipped lake trout planted in the four jurisdictional areas of Lake Superior.

	Minnesota		Wisconsin		Michigan		Ontario		Total	
Year	Age 0	Age 1 or older	Age 0	Age 1 or older	Age 0	Age 1 or older	Age 0	Age 1 or older	Age 0	Age 1 or older
1947							28		28	
1948							33		33	
1949										
1950							50		50	
1951										
1952			145	102	65				210	102
1953			133	80	139	69	50		322	149
1954			142	102	121	134			263	236
1955				103		61				164
1956				201						201
1957										
1958				184		298		538		1 020
1959				151		43		473		667
1960			49	161		393	50	396	99	950
1961				314		392	60	494	60	1 200
1962	77			493		775		508	77	1 776
1963	175			311	162	1 186		477	337	1 974
1964	38	182		743		1 196		472	38	2 593
1965	149	102		448		780		468	149	1 798
1966	151	208		377		2 218		450	151	3 253
1967	154	228	105	244		2 059		500	259	3 031
1968		377		239		2 260		500		3 376
1969		216		251		1 860		500		2 827
1970		226		204		1 944		501		2 875
1971		280		207		1 055		475		2 017
1972		293		259		1 063		491		2 106
1973		284		227		894		500		1 905
1974		304		436		888		465		2 093
1975		337		493		872		510		2 212
Totals										
Age 0	744		574		487		271		2076	
Age 1 or older		3037		6330		20 440		8718		38 525
Grand total										40 601

Materials and Methods

The basic data are the records of lake trout plantings and of the annual spring catches in standard gillnet assessment fisheries in Lake Superior. Both data sets have been maintained and collated by the Great Lakes Fishery Commission and its cooperating agencies. (See footnote to Table 2.)

Between 1947 and 1956, preliminary plantings showed fingerling survival to be vanishingly low and yearling lake trout were, therefore, routinely planted from 1958 on and have provided virtually all of the recruitment of hatchery fish to the lake. The variability in the numbers planted annually (Table 1) provides a wide range of planting intensities for correlation with subsequent observed abundances.

Annual estimates of the observed density of marketable lake trout have been expressed (Table 2) as catch per unit of effort (CPE) values for fish of hatchery origin and for all lake trout pooled. Since most were between ages IV and IX inclusive, those from the hatcheries were clearly the survivors of the yearling plantings 3–8 yr earlier. Hence, the means of the plantings over years Y-3–Y-8, expressed as densities per square mile (2.59 km^2) of inshore lake trout water (70 m deep or less) are provided in column 6 of Table 2 for comparison.

Empirical evidence that a strong correlation ($r = 0.87$–0.99) between the abundance of planted trout and the mean density of the plantings providing them does exist has recently been supplied for two time periods in the sequence treated in Table 2, 1966–69 and 1970–76 (Lawrie 1978). In fact, because of the scarcity of native trout, equally good correlations were obtained for all trout, planted and native, pooled. Analysis of covariance indicated that dfferences in the slopes of the four regressions were not significant and adoption of a common slope provided the following relationships:

(1) Hatchery trout 1966–69 $Y = -86.176 + 0.986\,X$

(2) Hatchery trout 1970–76 $Y = -30.678 + 0.986\,X$

(3) All trout 1966–69 $Y = -80.903 + 0.986\,X$

(4) All trout 1970–76 $Y = 8.608 + 0.986\,X$

where Y is the CPE in assessment nets and X the planting density.

TABLE 2. Lake trout abundance in the spring assessment fisheries in Lake Superior, proportion and abundance of hatchery trout, and the density of the plantings creating the stock.[a]

	No. of marketable lake trout per 10 000 ft (3048 m) of net	% hatchery trout	No. of marketable hatchery trout per 10 000 ft (3048 m) of net	Cumulative plantings Y-8 – Y-3	Mean annual plant/mi² (2.59 km²) of trout water
Michigan 2994 mi² (2.59 km²) of inshore trout water (<40 fathoms (73 m) deep)					
1962	39	27.1	11	536000	30
1963	46	40.3	19	795000	44
1964	43	70.6	30	1126000	63
1965	55	88.8	49	1901000	106
1966	75	95.4	72	3087000	172
1967	116	98.5	114	3985000	222
1968	245	99.5	244	4722000	263
1969	249	99.3	247	6547000	364
1970	441	98.4	434	8214000	457
1971	525	98.0	515	9699000	540
1972	574	96.0	551	10373000	577
1973	573	93.5	536	11121000	619
1974	406	92.5	376	11396000	634
1975	600	89.5	537	10241000	570
1976	543	87.4	475	9076000	505
1977	637	85.0	541	7704000	429
1978	422	78.0	329	6716000	374
Wisconsin 1397 mi² (2.59 km²) of inshore trout water (<40 fathoms (73 m) deep)					
1962	77	32.8	25	741000	88
1963	88	53.5	43	800000	95
1964	111	69.7	77	1011000	121
1965	134	83.5	112	1303000	155
1966	150	89.7	135	1614000	193
1967	181	93.1	169	2173000	259
1968					
1969	187	94.3	176	2686000	320
1970	368	89.8	330	2616000	312
1971	326	83.0	271	2362000	282
1972	263	77.0	203	2302000	275
1973	213	75.5	161	1763000	210
1974	220	80.1	176	1522000	182
1975	153	71.7	110	1404000	168
1976	182	75.5	137	1387000	165
1977	159	65.0	103	1584000	189
1978	174	65.0	113	1826000	218
Ontario 2672 mi² (2.59 km²) of inshore trout water (<40 fathoms (73 m) deep)					
1966	99	95.3	94	2886000	180
1967	111	98.1	109	2820000	176
1968	76	97.9	74	2815000	176
1969	90	96.8	87	2869000	179
1970	105	95.4	100	2926000	183

[a] Data on lake trout abundance to 1970 from the Annual Report of the Great Lakes Fishery Commission 1972, and for later years from the Minutes of the 1977 Annual Meeting of the Lake Superior Committee, Great Lakes Fishery Commission, Milwaukee, WI, Feb. 23, 1977. Data for Michigan and Wisconsin giving the percentage of hatchery fish in the assessment catches from Pycha and King (1975) to 1970 and from the files of the Ontario Ministry of Natural Resources to the same year. I am indebted to R. L. Pycha of the United States Fish and Wildlife Service for post 1970 "percent hatchery trout" figures for Michigan and Wisconsin. "Cumulative plantings" and "Mean Annual Plant/mi²" figures were derived from Table 1. Areas are those presented at the Annual Meeting of the Lake Superior Committee, Great Lakes Fishery Commission, Milwaukee, WI, March 8, 1966.

Between stanza changes in the "hatchery," regressions were interpreted as gains owing to improvements in survival since natural recruitment was clearly not involved. Conversely, changes in the within-stanza differences between "hatchery" and "all" trout regressions were considered to estimate changes in the abundance of native trout. The present paper extends that analysis.

Traditionally, catch per unit of effort has been held to be proportional to density so that:

(5) $C/f = qN/A$

where C/f is catch divided by effort; N/A, numbers divided

TABLE 3. Catch per unit of effort of Lake Superior lake trout (Y) in the spring assessment fisheries as a function of the Planting Density (X) 3–8 yr earlier. Two sets of regressions are presented for each of six time stanzas, one involving hatchery-reared trout only, the other for all trout, native and hatchery-reared together. **Difference significant, $P<0.001$.

Stanza	Hatchery trout regression	t	All trout regression	t
1962–66	$Y=0.559\,X$		$Y=0.699\,X$	
		0.827		0.629
1966–69	$Y=0.624\,X$		$Y=0.646\,X$	
		5.383**		6.206**
1970–75	$Y=0.916\,X$		$Y=0.994\,X$	
		0.068		0.371
1971–76	$Y=0.913\,X$		$Y=1.008\,X$	
		0.402		0.798
1972–77	$Y=0.934\,X$		$Y=1.054\,X$	
		0.183		0.216
1973–78	$Y=0.921\,X$		$Y=1.072\,X$	

by area, i.e. density; and q is the catchability coefficient (Gulland 1969).

However, in this case, density can also be thought of as reflecting the IV- to IX-yr-old survivors of the recruits to the area concerned. Given constant annual recruitment of R fish and a constant annual survival of S of them (expressed as a proportion), the survivors vulnerable to the assessment nets each year at the time of recruitment would be given by the difference between the sums to the ninth and third terms of the geometric series:

$$R + RS + RS^2 \ldots\ldots RS^8$$

which is

$$(6)\quad \left[\frac{(1-S^9)}{(1-S)} - \frac{(1-S^3)}{(1-S)}\right]R.$$

Obviously, the equalities

$$(7)\quad C/f = qN/A = q\left[\frac{(1-S^9)}{(1-S)} - \frac{(1-S^3)}{(1-S)}\right]\frac{R}{A}$$

should obtain, which is to say C/F (CPE) should be related to planting density by a linear function passing through the origin and having a slope of:

$$(8)\quad b = q\left[\frac{(1-S^9)}{(1-S)} - \frac{(1-S^3)}{(1-S)}\right]$$

which will clearly increase as S is increased unless there are compensatory changes in q.

Accordingly, despite the fact that the intercept model provided an excellent least squares fit to the 1966–76 data considered earlier, the analyses have been reiterated to include additional data from the extended time series 1962–78, a no-intercept model has been used, and regressions have been developed for six stanzas, 1962–66, 1966–69, 1970–75, 1971–76, 1972–77, and 1973–78, in hope of demonstrating secular changes. Minnesota data were not considered in the analyses because they did not span the early time periods deemed of greatest concern. In pooling data from the three jurisdictions listed in Table 2, those for Michigan in 1974 were omitted as they had already been shown to be anomalous (Lawrie 1978).

Results

Table 3 presents the regressions obtained by applying the no-intercept model to both the "hatchery" and "all" trout data of Table 2. Given the homogeneity of the data, irrespective of origin, they can be taken as representative of the lake as a whole. Also provided are "t values" to allow tests of significance of the successive differences in the slopes of the regressions in the two series. Although only the differences between the 1966–69 and 1970–75 stanzas are statistically significant (both with probabilities <0.001), it is apparent that lake trout survival increased rapidly and at an accelerating rate until the 1970s and thereafter has remained relatively constant.

These regressions allow computation of the expected CPEs for "all" trout, and for "hatchery" trout only, from any reasonable planting regime. Table 4 presents such estimates for a regime employing the means of the planting densities actually used by Michigan, Wisconsin, and Ontario through each time stanza thus simulating the "average" Lake Superior experience. It also partitions the estimated CPEs to demonstrate the contributions from changes in the postulated planting density, in the estimated post 1962–66 survival, and in the recruitment of native trout.

The estimates of "hatchery" lake trout CPEs owe nothing to natural reproduction. Changes in their values from stanza to stanza are a consequence of between-stanza changes in both planting density and survival (i.e. regression slope). Contributions from changes in planting density only have been estimated in row 6 of Table 4 as the products of successive within-stanza mean planting densities and the slope in the first, 1962–66, stanza. Contributions from the actual changes in survival in subsequent stanzas have then been derived as differences between the values of rows 3 and 6.

Estimates of native lake trout CPEs, row 4, are, of

TABLE 4. Calculations of CPEs for hatchery-reared and native Lake Superior lake trout in each stanza and the partitioning of these values into components owing to changes in planting densities, changes in survival, and changing recruitment from natural reproduction.

	Stanzas					
	1962–66	1966–69	1970–75	1971–76	1972–77	1973–78
1. Mean planting densities	113.4	227.6	364.6	372.1	353.6	329.9
2. Slopes of the "hatchery trout" regressions	0.559	0.624	0.916	0.913	0.934	0.921
3. Estimated CPEs "hatchery trout"	63	142	334	340	330	304
4. Estimated CPEs native trout	16	5	28	35	43	50
5. Estimated CPEs "all trout"	79	147	362	375	373	354
6. CPEs of "hatchery trout" owing solely to change in planting density		127	204	208	198	184
7. CPEs of "hatchery trout" owing solely to change in survival		15	130	132	132	120
8. CPEs of native trout owing solely to change in survival		0.5	11	14	17	20
9. CPEs of native trout owing to natural recruitment		4.5	17	21	26	30

course, differences between the values of rows 3 and 5. On the assumption that these native lake trout had been affected by changes in survival to the same extent as the hatchery fish, row 8 estimates the contributions to the CPEs of native fish from these changes. The values are simply the products of the CPEs of row 4 and the ratios of the corresponding values in rows 7 and 3. Row 9 derives the contribution to the CPEs of native lake trout in the form of recruits from natural reproduction as the differences between the values of rows 4 and 8.

To the extent that the example worked out in Table 4 is a reasonable simulation of events in Lake Superior during the 1960s and 1970s, we conclude that, of the increased lake trout abundance realized, on average, about 55% was owing to a trebling of the planting density, 40% to improved survival, and 5% to increasing recruitment of native lake trout. More important than the estimate of the average magnitude of the contribution from natural recruitment is the clear evidence (row 4, Table 4) that it is accelerating.

Discussion

The substantial improvement in survival of lake trout flagged by this analysis is, of course, of special interest, for it offers the hope that rehabilitation may ultimately be possible without support from the hatcheries or, at least, with much less support than has been required to date. Improvements in survival can be brought about because recruitment is expanding and the population growing, because there is an actual reduction in the number of deaths in the population, or both. In the Lake Superior situation both influences must surely have been at work, the former because of the massive and continuing planting program, the latter because of the success of the sea lamprey control program. For obvious reasons, a good deal of practical interest attaches to discriminating the effects of each activity.

The slopes of the "hatchery" trout regressions and the mean planting densities are, of course, autocorrelated so that the obvious (and demonstrable) correlation between rows 1 and 2 of Table 4 is neither surprising nor conclusive. Nonetheless, the analysis is representative in the sense of covering virtually the entire period over which the planting program has extended and the correlation is consistent with expectation.

In contrast, the analysis really does not allow a fully effective comparison between conditions before and after sea lamprey control was achieved in 1961/62. For the 1962–66 stanza mean planting densities were calculated for Michigan, Wisconsin, and Ontario for each year. Since for any one year these were based on the plantings in years Y-3–Y-8, a total of 69 records of plantings from the years 1954–63 (Table 1) were utilized. However, because sea lamprey-induced lake trout mortalities are minor before age IV (Pycha and King 1975) and sea lamprey numbers collapsed in mid-1961, only the plantings of 1958 or earlier were exposed to a half year, or more, of precontrol sea lamprey predation. Hence, for this earliest stanza, only 24 of the 69 plantings contributing to the analysis had experienced any precontrol predation and they averaged only 1.6 yr of exposure out of a possible 5. For the 1966–69 stanza, only 3 of 72 plantings had been exposed and then for no more than half a year. Hence, although the postcontrol situation is well described by the data from the 1970–75 to 1973–78 stanzas, comparisons which express the full impact of sea lamprey control do not appear possible.

We therefore conclude that the apparent changes in relative survival from the 1966–69 stanza on do not in any way reflect the major collapse in sea lamprey numbers in 1961/62. Although we cannot rule out a contribution from later small gains in sea lamprey control, it seems likely that the observed improvement was simply the direct result of the rapid growth in the recruitment of lake trout, especially hatchery-reared fish. The nonsignificant increase in apparent survival from 1962–66 to 1966–69 probably does owe something to the 1961/62 collapse in sea lamprey numbers, but the contribution from this source was certainly not large in absolute terms, or the increase in survival would surely have been significant. Considering the limited extent to which the 1962–66 analysis can represent the precontrol situation, it probably was not large even in relative terms. In any event, we cannot discriminate between the contributions from the two sources.

Finally, the problem which we have encountered, namely lack of data from a period sufficiently early to adequately represent precontrol conditions, appears likely to also frustrate attempts to reconstruct the past by other direct methods such as cohort analysis. Hence, it seems certain that demonstrations of the importance of sea lamprey predation and hence of the continuing control program must rest on contemporary evidence such as has been presented elsewhere in this symposium (Pycha 1980).

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GULLAND, J. A. 1969. Manual of methods for fish stock assessment. Part 1 Fish population analysis. FAO (F.A.O.U.N.) Man. Fish. Sci. 4: 154 p.

LAWRIE, A. H. 1978. The fish community of Lake Superior. J. Int. Assoc. Great Lakes Res. 4: 513–549.

LAWRIE, A. H., AND J. F. RAHRER. 1972. Lake Superior: effects of exploitation and introduction on the salmonid community. J. Fish. Res. Board Can. 29: 765–776.

PYCHA, R. L. 1980. Changes in mortality of lake trout (*Salvelinus namaycush*) in Michigan waters of Lake Superior in relation to sea lamprey (*Petromyzon marinus*) predation, 1968–77. Can. J. Fish. Aquat. Sci. 37: 2063–2073.

PYCHA, R. L., AND G. R. KING. 1975. Changes in the lake trout population of southern Lake Superior in relation to the fishery, the sea lamprey and stocking, 1950–70. Great Lakes Fish. Comm. Tech. Rep. 28: 1–34.

SMITH, B. R., AND J. J. TIBBLES. 1980. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936–78. Can. J. Fish. Aquat. Sci. 37: 1780–1801.

Changes in Mortality of Lake Trout (*Salvelinus namaycush*) in Michigan Waters of Lake Superior in Relation to Sea Lamprey (*Petromyzon marinus*) Predation, 1968–78[1,2]

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PYCHA, R. L. 1980. Changes in mortality of lake trout (*Salvelinus namaycush*) in Michigan waters of Lake Superior in relation to sea lamprey (*Petromyzon marinus*) predation, 1968–78. Can. J. Fish. Aquat. Sci. 37: 2063–2073.

Total mortality rates of lake trout (*Salvelinus namaycush*) of age VII and older from eastern Lake Superior were estimated from catch curves of age distributions each year in 1968–78. The instantaneous rate of total mortality Z varied from 0.62 to 2.31 in close synchrony with sea lamprey (*Petromyzon marinus*) wounding rates on lake trout. The regression of transformed Z on the index of lamprey wounding, accounted for over 89% of the variation in lake trout mortality ($r^2 = 0.893$). An iterative method of estimating rates of exploitation u, instantaneous rates of fishing mortality F, K (a constant relating sample catch per unit effort to population size), instantaneous normal natural mortality rate M, and instantaneous rate of mortality due to sea lamprey predation L from the sample catch per unit effort and total catch by the fishery is presented. A second method using the results of a 1970–71 tagging study to estimate the mean F in 1970–77 yielded closely similar results to the above and is presented as corroboration. The estimates of u, F, and M appear to be reasonable. F ranged from 0.17 in 1974 to 0.42 in 1969 and M was estimated at 0.26. L varied from 0.21 in 1974 to 1.70 in 1968. Management implications of various policies concerning sea lamprey control, exploitation, and stocking are discussed.

Key words: lake trout, sea lamprey, lamprey control, mortality, predation, Lake Superior, fishery, management

PYCHA, R. L. 1980. Changes in mortality of lake trout (*Salvelinus namaycush*) in Michigan waters of Lake Superior in relation to sea lamprey (*Petromyzon marinus*) predation, 1968–78. Can. J. Fish. Aquat. Sci. 37: 2063–2073.

Les taux de mortalité totale de touladis (*Salvelinus namaycush*) d'âge VII et plus en provenance du secteur est du lac Supérieur ont été estimés à partir des courbes de capture par âge à chacune des années 1968–78. Le taux instantané de mortalité totale Z varie de 0,62 à 2,31 en étroite concordance avec les taux de blessures causées par la grande lamproie marine (*Petromyzon marinus*) chez le touladi. La regression de Z transformé sur l'indice de blessures par les lamproies explique plus de 89% de la variation de la mortalité chez le touladi ($r^2 =$ 0,893). Le présent article décrit une méthode itérative d'estimation des taux d'exploitation u, taux instantanés de mortalité par pêche F, K (une constante faisant la relation entre prise par unité d'effort par échantillonnage et effectif de la population), taux instantané de mortalité naturelle normale M et, enfin, taux instantané de mortalité due à la prédation par la grande lamproie marine L à partir de la prise par unité d'effort par échantillonnage et des prises totales par pêche. Une second méthode, utilisant les résultats d'un programme d'étiquetage de 1970–71 effectué en vue d'éstimer le F moyen pour 1970–77, donne des résultats semblables à ceux de la première méthode et est présentée ici à titre de confirmation. Les estimations de u, F et M semblent raisonables. F varie de 0,17 en 1974 à 0,42 en 1969, et on estime M à 0,26. L varie de 0,21 en 1974 à 1,70 en 1968. Les implications quant à la gestion, les diverses politiques concernant le contrôle de la grande lamproie marine, l'exploitation et les peuplements sont analysés.

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Predation by the sea lamprey (*Petromyzon marinus*) has long been recognized as a causative factor in the decline and demise of lake trout (*Salvelinus namaycush*) in Lakes Huron and Michigan in the 1940s and 1950s and the decline of lake trout in Lake Superior in the 1950s and early 1960s. However, the evidence linking declines of lake trout with lamprey predation has been largely circumstantial. Fry (1953) was the only worker who documented a decline related to sea lampreys in a lake trout population that was not also subjected to intense commercial fishing. Eschmeyer (1957) showed that lake trout in Lake Michigan continued to decline in the presence of sea lampreys after the fishery collapsed. Budd et al. (1969) were the only workers able to account for fishing mortality and to relate changes in natural mortality to the incidence of lamprey marks (wounds and scars) on lake trout in the Great Lakes. However, their work was limited to South Bay, Lake Huron. In the late 1960s, I attempted to determine mortality rates due to sea lampreys from differences in total mortality rates found at various levels of sea lamprey wounding (Pycha 1970), but was unsuccessful. I could not separate fishing from natural mortality because information on the magnitude of and the size and age composition of the catch was lacking.

In 1968–78, however, enough data became available to make attempts to estimate mortality components. In that period, during which the incidence of sea lamprey wounds on lake trout varied by as much as threefold, enough lake trout survived for 3 or more years of full vulnerability to our lake trout sampling gear to make possible the estimation of total mortality rates from annual age distributions with reasonable accuracy. Furthermore, a postcard creel census begun by the Michigan Department of Natural Resources (MDNR) in 1969 yielded the first estimate of the total sport fishing catch. The Department also developed indirect methods of checking on unreported commercial catches by the Indian Treaty gillnet fishery. The available data on lake trout catches along with accumulated nonquantitative and semiquantitative field observations enabled me to make total catch estimates as far back as 1966.

The purposes of this study are to illustrate changes in total mortality of lake trout in relation to changes in the incidence of sea lamprey wounds; to present two methods for apportioning total mortality into components due to lamprey predation, other natural causes, and fishing; to make estimates of these mortality components from the available quantitative data and supporting general information; and to examine the implications of these estimates for fishery management.

The Problem, Assumptions, and Biases

A number of difficulties have plagued all workers who have attempted to evaluate the effects of sea lamprey predation on lake trout. Foremost is that usually only the survivors of lamprey attacks bearing wounds or scars are seen. The incidence of wounds on lake trout is obviously related in some way to attack rates, but the relation of wounding rates to either attack rates or mortality is unclear (Pycha and King 1975). Wounding rates vary with time of year, size of lake trout, and almost certainly the predator–prey ratio. The relation of wounding to mortality of prey may also vary with any or all of these variables.

Gill nets have been the only practical fishing gear for sampling lake trout in most of Lake Superior and, for economy, all large-scale sampling has been done by commercial fishermen using commercial 11.43-cm-mesh gill nets. Gill nets fished for most species are highly size-selective, but about half the lake trout caught are entangled by their teeth, other mouthparts, or fins, and the selectivity range is, thus, wide. Pycha (1970) stated that the selectivity of 11.4-cm gill nets for lake trout appeared to be nearly equal for all lengths of lake trout between 50.8 and 76.2 cm long, but an uncompleted analysis of an experimental net selectivity study (J. H. Selgeby, Ashland Biological Station, Wisconsin, personal communication) suggests that 11.4-cm gill nets have a peak efficiency for lake trout 48–53 cm long and that efficiency declines gradually below 48 cm and above 53 cm. The experimental fishing for the net selectivity study was done with nets hung on the one-half basis, but commercial gill nets are all hung fuller than our experimental nets to give them greater entangling power. The commercial gill nets from which my lake trout samples were obtained should have been less size-selective than those used experimentally, but their selectivity has not been defined. I believe that size selectivity does not seriously bias mortality estimates for the age-groups considered in this study. Any bias due to net selectivity would cause overestimation of total mortality rates. Since catches in 1974–78 contained a higher proportion of fish longer than 76 cm than did those in 1968–73, bias due to net selectivity could possibly extend across years. The effect of an across-years bias would be to underestimate the slope of the regression of total mortality rate on lamprey wounding rate and would overestimate natural mortality rate in the following analysis.

In the late 1960s, I attempted to determine total mortality rates of various cohorts of lake trout (marked with clipped fins that designated location and year of stocking) from the catch per unit effort (C/f) of that cohort in successive years after age VI (Pycha 1970). Annual mortality rates between ages were plotted against the spring lamprey wounding rate of the cohort each year. A positive relation between wounding rate and mortality was apparent, but the range of mortality rates at the highest levels of wounding was excessively broad, because of possibly either small sample numbers of the larger, older fish or to fluctuations in C/f caused by variations in availability. The annual total mortality rate A of 0.26 at the intercept of the Y axis was an estimate of the combined conditional rates of normal natural mortality n and fishing mortality m if no mortality due to lamprey predation existed, but I had no means of separating fishing from normal natural mortality.

Further attempts to determine total mortality rates by the above method led to the conclusion that fluctuations in C/f of individual cohorts of stocked lake trout were too large to permit reliable estimates to be made. Occasional negative mortality rates led to a suspicion that sampling error was the cause of the difficulty, but a general depression of both the C/f and the total annual catch of all cohorts in 1974 followed by a recovery to higher C/f values and catch in 1975 suggested that availability of lake trout may vary from year to year.

Catch curves derived from age distributions within years avoid the difficulties caused by variations in C/f, but are subject to irregularities caused by variations in year-class strengths. Since most of the lake trout in Lake Superior in 1968–78 were finclipped stocked fish, compensation for differences in year-class strengths due to differences in numbers stocked was possible. Effort was therefore concentrated on determining age distributions in years in which lamprey wounding rates were relatively high or low. Initial results suggested that lamprey wounding rates were positively correlated with average total mortality rates as estimated from the right-hand limbs of the catch curves, and completion of an 11-yr series yielded further confirmation that led to the analysis presented here.

Since the size-range of lake trout bearing sea lamprey wounds (43 cm and longer) is almost identical with that caught by 11.43-cm gill nets and also to that taken by the sport fishery, knowledge of fishing mortality is needed for sound estimation of mortality due to sea lampreys. In 1970, we began a tagging study to obtain an estimate of fishing mortality in Michigan waters, but the high cost and difficulty of obtaining large numbers of uninjured lake trout from trap nets forced discontinuance of the study.

Two methods of estimating fishing mortality are used in this study. Both use total catch in the sport and commercial fisheries and C/f, and involve the assumption that C/f is a true measure of relative abundance of lake trout. C/f of all cohorts of finclipped fish of all ages combined is probably less sensitive to random sampling error than is C/f of individual cohorts of a single age, but the evidence of error due to a change in availability in 1974 casts some doubt as to the accuracy of C/f as a measure of relative abundance in any single year. Even if errors due to sampling or changes in availability are relatively large, such errors should tend to be offsetting over a period of several years. The first method of estimating fishing mortality is based on an assumption that C/f is a reasonably accurate estimator of relative abundance each year. The second method is based on the less rigorous assumption that an average of C/f over several years is a reasonably good estimator of mean relative abundance, but the actual estimation of fishing mortality requires use of the results of the small amount of tagging done in 1970. The statistical confidence limits on the returns from that tagging are, however, narrow enough to lend credence to the results. As with all tagging studies, any failure of fishermen to report tagged fish caught would result in underestimation of fishing mortality rate which, in turn, would result in overestimation of normal natural mortality.

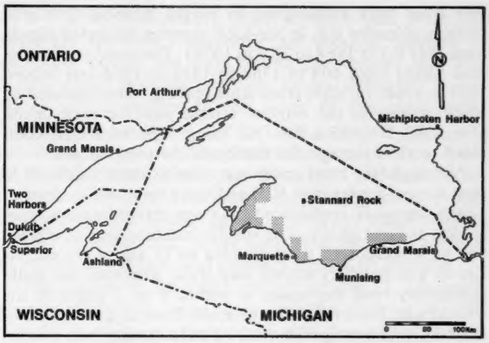

FIG. 1. Locations sampled for lake trout (shaded areas) in Michigan waters of Lake Superior, 1967–78.

Materials and Methods

Total mortality rates of lake trout were determined from spring (mainly May) samples collected by five commercial fishermen who operated under permits issued by MDNR in inshore areas from the east side of the Keweenaw Peninsula to a point about 30 km east of Grand Marais, Michigan (Fig. 1). The 1972 sample, however, came from only four fishermen because no fishing was done in the area off Munising. Each fisherman fished gillnet gangs of specified length (usually 457 or 914 m) and mesh (11.4 cm, stretched measure) at several locations. The nets were usually lifted after three nights in the water and at least six lifts (usually considerably more) were made by each fisherman. Since total catches as well as gear were limited, the samplers who had the poorest fishing lifted the largest amounts of gear. The total length of sampling net lifted varied from 29 261 m in 1972 to 136 489 m in 1968, and the number of fish taken in the spring sampling from 4931 in 1972 to 9852 in 1970 (total in 1968–78, 80 067). All lake trout caught were measured and checked for missing (clipped) fins (indicating that they were of hatchery origin) and lamprey wounds and scars. Scale samples were taken from all fish 63.5 cm long or longer, and a net-run sample was taken from those shorter than 63.5 cm.

Because most lake trout caught in Lake Superior were marked with clipped fins or combinations of two or more clipped fins, none of which was used anywhere in the lake more than once every 2 years (a few clips were used only once), fish bearing a specific finclip usually belonged to one of only two or three age-groups. Clipped fins were used to denote both years of planting and location of planting (by state or province). To simplify age determinations, scale samples were separated according to clipped fins and subsampled by 2.54-cm-length intervals — either 20 fish per interval or all fish in the interval if less than 20 fish. Native lake trout were subsampled by length intervals (the percentage of native fish in the total samples increased slowly from only 0.3 in 1968 to 22.5 in 1978). The number of scales read varied from 604 in 1968 to 1562 in 1976 and totaled 9635 in 1968–78. Ages from scale reading were expanded by length-groups to the original sample size for each finclip group and the native fish. All the groups were then combined to yield the age distribution of the total sample.

Although lake trout scales are often extremely difficult to read at ages greater than VIII or IX, we were able to develop a high degree of confidence in our age determinations, even at ages as great as XV. The specific combinations of clipped fins on stocked lake trout enabled us to assign the correct age to any hatchery-reared lake trout whenever we could confidently read the scales to within 1 or 2 years of the correct age. The availability of scales from large numbers of essentially known-age fish enabled us to develop new criteria for identifying annuli at the older ages. After we reached the point where we could read scales without knowing the finclip combination and arrive at the exact age designated by the clipped fins in a high percentage of the trials, we felt confident that we could determine ages of native (not finclipped) fish within 1 year and finclipped fish exactly for most of our samples.

Catch curves of the age distributions in some years were highly irregular because of at least in part, wide fluctuations in year-class strengths. Since the stocking rate in the sampling area varied roughly sixfold (from 300 000 to 1 720 000) for the year-classes considered here, the age distributions were adjusted for an assumed constant stocking rate of one million fish per year. The adjustments involve an assumption that survival from time of stocking to full vulnerability to the sampling gear was constant for all year-classes. Lawrie (1980) provided strong evidence that C/f in the fishery was linearly related to stocking rate in earlier years which suggests the assumption is reasonable. The adjustments of the age distributions for stocking rates smoothed the right hand limbs of the catch curves enough to indicate they could be adequately described by straight lines.

Since rates of immigration into and emigration from the sampling area were unknown, an assumption was made that they were offsetting. An examination of changes in the percentages of lake trout with site-specific finclips taken at various sampling locations suggested that dispersal from stocking sites in the sampling area was completed by age VII and movements thereafter were random.

Catch curves of the adjusted age distributions all had typical ascending left limbs, dome-shaped center portions, and descending right limbs. The apparent age of full vulnerability to the gear, however, varied from VII to IX. The age at full vulnerability was estimated by inspection. In most years the transition from the dome-shaped center portion of the catch curve to the roughly straight right-hand limb was easily discernible. In most years also, the oldest one or two age-groups in the catch fell off sharply, which suggested that mortality of the oldest fish was very high. This apparent high mortality of the oldest age-groups occurred even in the earlier years when the oldest fish were of a size well within the high selectivity range of the sampling gear. Older age-groups that contained fewer than 10 fish were disregarded. Straight lines were fitted to the natural logarithms of the numbers of fish in the fully vulnerable age-groups by the method of least squares.

A real change in the age of full vulnerability could be caused only by a real change in growth rate or by a change in the fishing gear, neither of which accounts for the differences encountered here. A change in the apparent age of vulnerability could be caused by fluctuations in year-class strengths not compensated for by the adjustments for stocking rate or a change in a size-selective mortality factor such as sea lamprey predation that could alter the apparent growth rate. Pycha (1970) demonstrated that the length range at a given age of hatchery-reared stocked lake trout was large, recruitment into the fishery occurred over several years, and mortality of the larger, faster-growing members of a year-class was much higher than of the smaller, slower-growing members. Under these circumstances, high mortality due to lamprey predation on the larger, faster-growing fish could reduce the apparent growth rate and increase the apparent age for full vulnerability. I believe that it is more than coincidence that the years when the fully vulnerable age was IX were also years of high sea lamprey activity.

Sea lamprey wounding rates on lake trout were chosen as the index of lamprey predation for this study because a long series of comparable data was available and because wounding rates (as compared with estimates of lamprey abundance) probably reflect compensation for changes in the ratio between predator and prey or between predator and alternate prey. The index of sea lamprey wounding used in this study is the unweighted mean of the percentages of lake trout bearing unhealed lamprey wounds in three length groups: 53.3–63.3 cm, 63.4–73.5 cm, and 73.6 cm and longer. These intervals cover the length range of the age-groups used in mortality estimates. Unweighted means were used to maintain comparability of the index of wounding over a period of years when large changes occurred in the proportions of fish in the various length intervals.

The index of relative abundance used in estimating fishing mortality was the unweighted mean of the average C/f of each of the five sampler fishermen. Total sample catch/total sampling effort would have biased the index in favor of the fisherman with the lowest C/f.

In June and July 1970, a total of 278 lake trout, 50.8 cm and longer, were tagged with plastic bird bands around the lower jaw. All fish were released near Marquette and Munising, Michigan, and came from trap nets fished for lake whitefish (*Coregonus clupeaformis*). By the end of July 1971, a total of 30 tag returns had been reported by commercial fisherman and anglers. All tag returns came from within the study area.

Annual catch estimates (Table 1) for the Michigan sport fishery from a postcard census in 1969–78 were provided by Mercer H. Patriarche (MDNR, Ann Arbor, Michigan). Sport catch estimates by localities that could be summarized to correspond to the area covered in this study were available only for 1972–76, and 1978. Estimates of the sport catch in the study area in other years were based on an assumption that annual changes in the sport catch within the study area were proportional to changes in the total sport catch. Sport catch estimates for 1966–68 were based on field observations, which suggested that the catch roughly doubled each year in 1964–69 (Asa T. Wright, MDNR, Lansing, Michigan, personal communication).

Incidental catch data for lake trout caught in 11.4 cm-mesh gill nets fished for lake whitefish in 1971–78 were provided by Richard Schorfhaar (MDNH, Lansing, Michigan) from departmental records of landings and sales; he also provided estimates of the average weights of lake trout taken in incidental catches and by the sport fishery. Incidental catch data for lake trout caught in 6.4-cm-mesh gill nets

TABLE 1. Estimated numbers of lake trout taken by various fisheries between the Keweenaw Peninsula and Grand Marais, Michigan, 1966–77.

Year	Sport	Assessment	Indian Treaty	Incidental
1966	16 250	15 687		4900
1967	32 500	19 247		4900
1968	65 000	17 472		4900
1969	130 136	18 274		4783
1970	130 424	10 886		3154
1971	108 679	10 319	7 500	4768
1972	92 480	8 224	11 000	2415
1973	143 100	14 360	14 500	2149
1974	106 200	6 218	18 125	2186
1975	160 650	5 495	23 192	2807
1976	178 400	8 694	33 368	3600
1977	121 342	7 401	45 902	741

fished for ciscoes (*Coregonus* sp.) were provided by the Great Lakes Fishery Laboratory, Ann Arbor, Michigan. Estimates of incidental catches in 1968–70 were provided by Asa T. Wright and those for 1966–67 were assumed to have been equal to the 1968 catch.

Estimates of catches by the Indian Treaty gillnet fishery (which was not required to report catches to MDNR) were obtained from departmental records of purchases of lake trout from treaty fishermen by licensed wholesale fish dealers in 1976–78. Estimates for 1971–75 were made by back extrapolation of the 1976–78 trend of increase in the reported catch.

The accuracy of estimates of the total catch of lake trout in the study area is obviously unknown. The 95% confidence limits for the postcard creel census catch estimates for the entire sport fishery were approximately ±40% in most years (Mercer H. Patriarche, personal communication). Estimates of the catch within the sampling area were even less precise. In addition, on-site creel census checks on the sport catch in recent years suggest that the postcard census is biased toward larger estimates than the actual catch. This bias may be as large as 50% (Richard Schorfhaar, personal communication). The estimate of the catch by Indian Treaty fishermen is an underestimate because many lake trout were sold directly to retail outlets or outside the State of Michigan. The magnitude of the errors varies with locality, but no reasonable estimate of the errors was available. The data on incidental catches, except for those in 1966–68, are believed to be reasonably accurate, and the catch data on the lake trout assessment (sampling) fishery are almost exact.

Total Mortality in Relation to Sea Lamprey Predation

Total annual mortality A varied from a maximum of 0.90 in 1968 to a minimum of 0.46 in 1974 (Fig. 2). The percentage of lake trout with unhealed wounds rose sharply from a relatively low level in 1967 to a high level in 1968, declined to another low in 1970, and increased again to a high level in 1971–73 (Fig. 3). In 1974, wounding rate fell to its lowest level during the period, and increased only slightly in 1975–78.

Catch curves from age distributions should reflect the past mortality history of the age-groups (Ricker 1975). If total mortality rates within a year were the same for all fully vulnerable age-groups, changes in mortality during the year before the sample was collected would be reflected only by an inflection in the curve and a change in the slope of the curve only between the youngest and next to youngest fully vulnerable age-groups. The slope of a straight line fitted to the logarithms of the age–frequency yields an average mortality rate over past years. Sharp year-to-year changes in the slopes of such average catch curves should be dampened in the same manner as in a series of running averages and changes should be gradual.

The slopes of the catch curves of Fig. 2, however, change sharply in some years, and the changes are obviously in close synchrony with the changes in the sea lamprey wounding rates of Fig. 3. The synchrony of changes in mortality rates and lamprey wounding rates suggests an explanation for the unexpectedly rapid changes in the slopes of the calculated average catch curves. If evidence is correct that mortality of lake trout due to sea lamprey predation increases with size of the trout (Budd et al. 1969; Pycha 1970; Pycha and King 1975), changes in the amount of sea lamprey predation would immediately alter the slope of an entire catch curve and, thus, the average slope. If mortality due to sea lamprey predation made up a substantial proportion of the total mortality, a calculated average catch curve would then reflect mainly mortality during the year before the age sample was taken rather than average mortality over past years. I believe that such is the case in this study. I also believe that the strong positive relation between the slopes of the catch curves and lamprey wounding rates may, in itself, be further confirmation of evidence that mortality of lake trout due to lamprey predation increases with size and age of lake trout. If lamprey-induced mortality were higher among younger and smaller lake trout than among the older and larger fish, an increase in lamprey predation would immediately cause the opposite effect of that seen in Fig. 2 and would reduce the slope of the catch curve.

An arithmetic plot of the instantaneous rate of total mortality Z of lake trout on the index of sea lamprey wounding was clearly not linear. A semilogarithmic plot of Z versus wounding appeared to be reasonably close to linear, and variance appeared (by inspection) to be homogeneous. When a straight line was fitted to the data by the method of least squares, the fit of the points to the line was reasonably good ($r^2 = 0.893$). When the slope of the line and the intercept were adjusted to those of a geometric mean functional regression (Fig. 4), the regression line intercepted the Y axis at an instantaneous mortality rate of 0.41.

If an assumption were justified that both normal natural mortality M (that due to natural causes other than sea lamprey predation) and fishing mortality F were constant in 1968–78, the instantaneous rate of mortality due to sea lamprey predation L at any level of wounding that pertained in those years could be

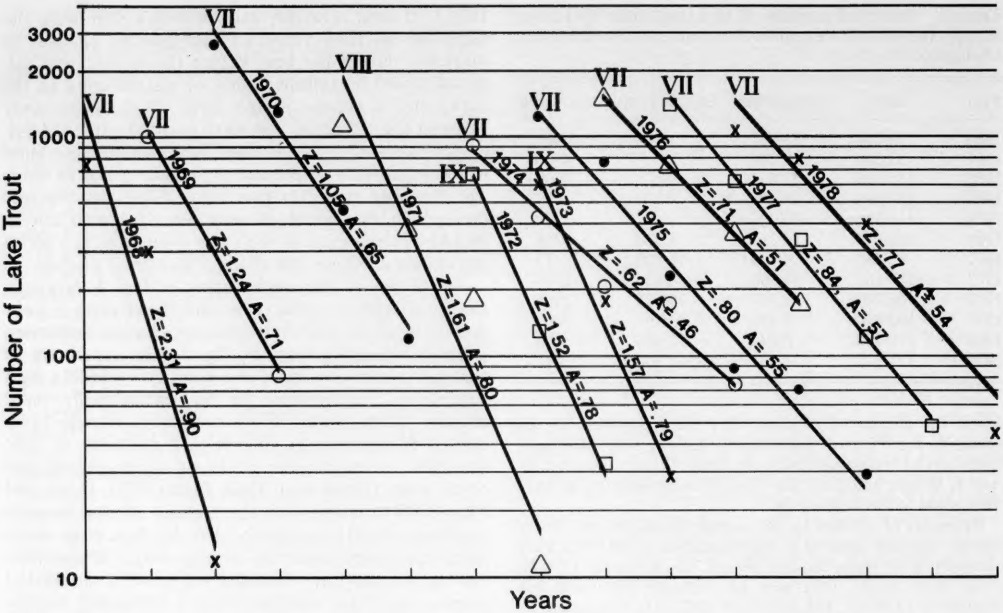

FIG. 2. Catch curves, instantaneous total mortality rates (Z), and total annual mortality rates (A), of lake trout caught in the spring, 1968–78.

estimated by subtracting 0.41 from the appropriate point on the regression line. An assumption of constant fishing mortality rate during a period of known expansion of both sport and commercial fishing cannot, however, be accepted without examination.

Estimation of Mortality Components

If normal natural mortality was constant in 1968–78 and the variation around the regression line in Fig. 4 was due mainly to variations in fishing mortality, most of the variability in the data could be removed and both normal natural mortality M and that due to sea lamprey predation L could be estimated by subtracting the applicable prior average value of F from that year's value of Z. A regression line of the correct form fitted to a plot of the above residuals versus the index of lamprey wounding should have a value of r^2 approaching 1.0, the Y-axis intercept would be the value of M, and the difference between points on the regression line and M would be the value of L at any given index of lamprey wounding. Unfortunately, the only direct measure of fishing mortality existing was a small-scale tagging study in 1 year.

The only substantial available data from which annual estimates of F could be obtained were those on the number of lake trout caught per unit effort in the spring assessment sampling fishery (C_i/f_i, where C_i = number caught over a short period and f_i = effort expended to obtain C_i) and those on estimated numbers of lake trout in the total annual catches (C_T) from Table 2.

Since C_i/f_i was obtained during a short period at the beginning of the season, it represents some fraction of the initial population N at the beginning of the season. Therefore:

$$(C_i/f_i)K = N$$

where K = a constant, and N = the number of vulnerable-sized fish in the population at the beginning of the fishing season. If all of the total annual catch were taken before growth and recruitment began, then

$$\frac{C_T}{N} = u, \text{ the rate of exploitation}$$

or

$$\frac{C_T}{(C_i/f_i)K} = u.$$

A large part of the total catch of lake trout is taken before growth and recruitment begin because most growth of lake trout of the age-groups fully vulnerable to the fishery occurs after September (Rahrer 1967). Since some recruitment occurs before the entire catch is taken, the above expression is an overestimate of u.

Estimates of total annual mortality A and instan-

TABLE 2. Example of statistics used in calculation of $Z_t - [(F_{t-1} + F_{t-2})/2]$ from the relations $C_T/(C_i/f_i)K = u$, and $F = uz/A$, for a value of $K = 7718.00$.

Year	C_T	C_i/f_i	$C_T/(C_i/f_i)$	u	Z	A	F	$(F_{t-1} + F_{t-2})/2$	$Z_t - [(F_{t-1} + F_{t-2})/2]$
1966	36 837	24.57	1499.26	0.194	1.43	0.76	0.365	—	—
1967	56 647	38.06	1488.36	0.193	0.99	0.63	0.304	—	—
1968	87 372	80.22	1089.15	0.141	2.31	0.90	0.362	0.334	1.98
1969	153 193	81.69	1875.29	0.243	1.24	0.71	0.424	0.333	0.91
1970	144 464	140.55	1027.84	0.133	1.05	0.65	0.215	0.393	0.66
1971	131 266	161.35	813.54	0.105	1.61	0.80	0.211	0.320	1.29
1972	114 119	167.36	681.88	0.088	1.52	0.78	0.171	0.213	1.31
1973	174 109	187.99	926.16	0.120	1.57	0.79	0.238	0.191	1.38
1974	132 729	133.14	996.91	0.129	0.62	0.46	0.173	0.205	0.42
1975	192 144	196.68	976.94	0.127	0.80	0.55	0.185	0.206	0.59
1976	224 062	178.12	1257.93	0.163	0.71	0.51	0.228	0.179	0.53
1977	175 386	208.53	841.05	0.109	0.84	0.57	0.161	0.207	0.63
1978	—	—	—	—	0.77	—	—	0.195	0.58

taneous rates of total mortality Z from the catch curves, total annual catch, C_T, and C_i/f_i provide all the necessary statistics, except K, for computation of the instantaneous rate of fishing mortality F from the following: $F = uZ/A$.

If the variation around the regression line in Fig. 4 is due largely to variations in fishing mortality, an approximation of K should be obtainable by iteration. Since the catch curves came from samples taken at the beginning of the fishing season (in years t), variations in the slopes of the catch curves due to variations in fishing mortality should be the result of fishing in all the prior years that affected the slopes of the curves. Because the effect of size-selective lamprey predation would tend to mask the effect of fishing in prior years, fishing in each year earlier than $t - 1$ would be expected to have a progressively smaller and possibly undetectable effect on the slopes of the catch curves. I was unable to devise a rational system for weighting the effects of fishing in progressively earlier years.

Trial values of K were obtained from assumed values of u in 1973, the year of fishing that should have had the greatest effect on the value of Z in 1974 which was the year of lowest total mortality rate. Trial values of K were used to calculate $Z_t - F_{t-1}$ for 1968–78 and were also used to calculate $Z_t - [(F_{t-1} + F_{t-2})/2]$ to test whether accounting for fishing in two prior years further reduced variability. The values of Z needed for calculation of F in 1966 and 1967 were estimated from the regression line of Fig. 4 at the applicable lamprey wounding rate. An example of a trial computation of $Z_t - [(F_{t-1} + F_{t-2})/2]$ at the best estimate value of $K = 7718$ is given in Table 2.

Regressions of the natural logarithms of $Z_t - F_{t-1}$ and $Z_t - [(F_{t-1} + F_{t-2})/2]$ on the index of lamprey wounding, regression coefficients r, and the r^2 values were calculated for each regression for each value of K derived from assumed 1973 values of u ranging from 0.08 to 0.16 by increments of 0.001. The values of r^2 for all trials were higher than the value of $r^2 = 0.893$

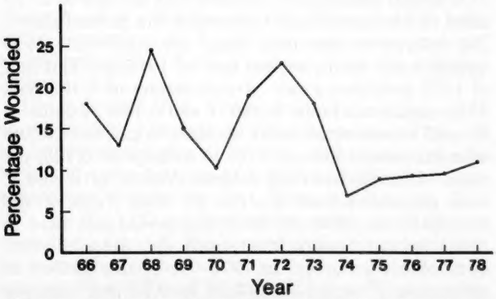

FIG. 3. Percentage index of wounding of lake trout by sea lampreys in the spring sampling area, Michigan waters of Lake Superior, 1966–78.

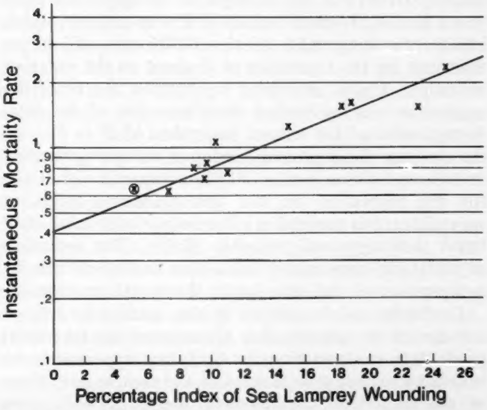

FIG. 4. Relationship of sea lamprey wounding rate on lake trout to instantaneous total mortality rate, Z, Michigan waters of Lake Superior, 1968–78.

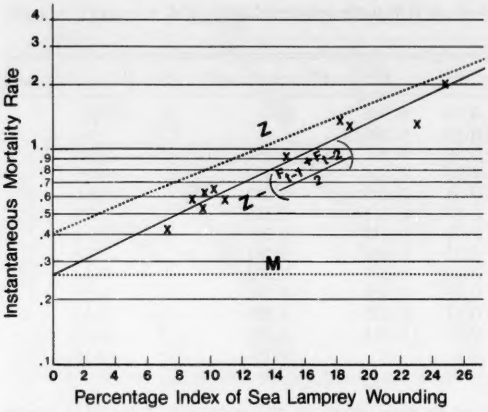

FIG. 5. Relation of sea lamprey wounding rate to Z (short dashed line), $Z_t - [(F_{t-1} + F_{t-2})/2]$ (solid line), and M (broken line), Michigan waters of Lake Superior, 1968–78.

for the regression of the natural logarithm of Z on the index of lamprey wounding. Those for the regression of $Z_t - [(F_{t-1} + F_{t-2})/2]$ on wounding were higher than those using $Z_t - F_{t-1}$. As expected, the r^2 values increased to a peak and then declined. At the peak value of $r^2 = 0.935$, K had a value of 7718 which is the best estimate of K obtainable by this method. The regression line of the natural logarithm of $Z_t - [(F_{t-1} + F_{t-2})/2]$ on the index of lamprey wounding was converted to that of a geometric mean functional regression to yield a Y-axis intercept of 0.26, the best estimate of M obtainable by this method (Fig. 5).

An attempt to reduce variability further by subtracting (from Z_t) the averages of all applicable prior ($t-1$ to $t-5$) years' values of F was not successful, but the resulting value of $r^2 = 0.926$ was still larger than that for the regression of Z alone on the index of wounding. I also attempted to improve the fit of the regression lines by further transformation of the data. A regression of the natural logarithm of $Z_t - F_{t-1}$ on the arcsin of the percentage index of wounding resulted in an increased value of r^2 (0.929 compared with 0.913 for the regression on the untransformed index of wounding), but resulted in a Y-axis intercept value of M lower than appeared plausible (0.09). The reduction of variability appeared to have been caused entirely by compression of the data due to the transformation.

Evaluation of the results of this method is difficult because of the questionable accuracy of the lake trout catch data and variations in C_i/f_i that appeared to be unrelated to both population size and sample size. None of the regression coefficients r for Z, $Z_t - F_{t-1}$, or $Z_t - [(F_{t-1} + F_{t-2})/2]$ was significantly different from any of the others, but all were significantly different from zero ($P < 0.001$). The Y-axis intercept estimate of $M = 0.26$ had 95% confidence limits of 0.15 and 0.46.

A possibility exists that the method described above is more precise than the results indicate. As mentioned earlier, the 1972 sample is not strictly comparable with those from other years because no sample was taken in the area near Munising, Michigan. In addition, 1972 had an extremely late spawning run of sea lampreys that was probably caused by unusual ice conditions in the lake (Harry H. Moore, U.S. Fish & Wildlife Service, Marquette, Michigan, personal communication). The effect of the lack of inclusion of the Munising sample is obviously unknown. The effect of a very late lamprey spawning run should have been to increase the proportion of lamprey marks recorded as wounds rather than scars. Recomputation of the regressions of Z and $Z_t - [(F_{t-1} + F_{t-2})/2)]$ against the index of lamprey wounding with 1972 eliminated from the data series yielded considerably higher values of r^2 (0.937 and 0.966, respectively). The 95% confidence limits of the estimate of $M = 0.24$ were 0.16 and 0.37.

A strong and significant relation between total mortality rate and sea lamprey wounding is apparent whether 1972 data are used or not. More than 89%, and possibly as much as 93.5% of the variation in total mortality rate is accounted for by variation in sea lamprey predation as reflected in wounding rates. Further reduction of variability by accounting for fishing mortality in two previous years appears to be a reasonable technique even though the reduction of variability was not significantly different statistically from that achieved by accounting for sea lamprey predation alone. Sea lamprey predation and fishing together accounted for 93.5% and possibly as much as 96.6% of the variation in mortality of lake trout in 1968–78. The method yielded estimated values of $M = 0.26$ or 0.24 (depending on whether the questionable 1972 data were used) that are reasonably or very close to the value Budd et al. (1969) believed was the most reasonable estimate of normal natural mortality of stocked lake trout in South Bay, Lake Huron (their annual mortality rate of 0.20 corresponds to $M = 0.223$).

A similar but different method was devised to avoid some of the assumptions involved in the method above. The returns of lake trout from our small-scale 1970 tagging study in the second half of 1970 and first half of 1971 indicated a rate of exploitation of 0.108 with 95% confidence limits of 0.071 and 0.144. A value of $K = 8534$ was obtained by iteration to calculate values of u that would give a 1970–71 average of 0.108, the value obtained from tag returns. Values of u and F were calculated from $C_T/(C_i/f_i)$ from Table 2 and $K = 8534$ for 1970–77. Only this period was used to avoid the early years when catch data were of more questionable accuracy. In 1970–77, by this method of estimation, F varied from 0.15 to 0.22 and averaged 0.18. As can be seen from Table 2, no trend in F is apparent in 1970–77. Whether fluctuations in F during these years were real or were due largely to sampling

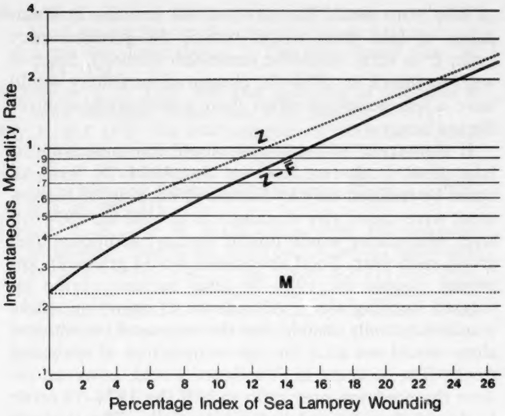

FIG. 6. Relation of sea lamprey wounding rate to Z in 1968–78 (short dashed line), $Z - \bar{F}$ in 1970–77 (solid line), and M (broken line), Michigan waters of Lake Superior.

error in C/f and /or to changes in C/f and C_T due to changes in availability is unknown. Regardless, an 8-yr average of F should be reasonably close to the true average. If we accept the regression line of Z on percentage wounded and the 1970–77 average F as reasonable, we need only subtract 0.18 from Z to obtain M (Fig. 6). The result is very similar to that from the earlier method. The Y-axis intercept estimate of M is 0.23 with 95% confidence limits (calculated from the confidence limits for the 1970–71 tag returns) of 0.17 and 0.29.

One serious flaw in the available data and a possible source of major error in the analyses is lack of Z values at percentage indices of lamprey wounding below 7.3 that necessitates extrapolation below that value. A major change in the form of the regression of Z on lamprey wounding would, obviously, alter the estimates of M. In 1979, the index of lamprey wounding at one major sampling and fishing port (Marquette) was only 5.2. A catch curve from the 1979 spring sample at Marquette had a Z value of 0.65. This point has been added (encircled) to Fig. 4 and lends some credence to the estimation of the Y-axis intercept by extrapolation.

The estimates of Z, F, and M, therefore, appear to be reasonable. The best estimate of mortality due to sea lamprey predation L from the first method should be the difference between $M = 0.26$ (possibly 0.24) and appropriate points on the regression line of $Z - [(F_{t-1} + F_{t-2})/2]$ at any given index of lamprey wounding (Fig. 5). The second method yields similar but somewhat higher values of L from the difference between $M = 0.23$ and points on the $Z - \bar{F}$ line.

The estimated instantaneous rate of mortality due to sea lamprey predation L in 1968–78 (from the first method) ranged from a low of 0.22 when the index of sea lamprey wounding was 7.3% (in 1974) to a high of 1.70 when the wounding index was 24.7% (in 1968). These instantaneous rates correspond to conditional mortality rates of 0.20 and 0.82, respectively. The instantaneous rate of fishing mortality F ranged from 0.17 in 1974 to 0.42 in 1969 (conditional rates of 0.16 and 0.34, respectively). The instantaneous rate of natural mortality M is assumed to have remained constant in 1968–78 at 0.26 (conditional rate of 0.23).

The estimates of L presented here are neither size- nor age-specific but are averages for all lake trout of age VII and older. Evidence has accumulated that mortality of lake trout due to sea lamprey predation is size- and age-specific and such a relationship is necessary to rationalize the changes in total mortality rates observed here. Efforts by colleagues are currently underway to modify this first approximation into size- and age-specific rates of lamprey-induced mortality within years. Results of these efforts are not yet available.

Management Implications

Restoration of self-sustaining lake trout stocks is the stated objective of every agency concerned with fishery rehabilitation in the upper Great Lakes. Data on lake trout stocks from both the prelamprey period and the period covered by this study are inadequate for development of reproduction curves and determination of the size of spawning stocks required. Management implications must, unfortunately, be drawn without adequate knowledge of necessary spawning stock size, even though rebuilding adequate spawning stocks is obviously necessary for attainment of the stated objective.

The results of this study suggest that during most of 1968–78 predation by sea lampreys was the single most important factor affecting mortality of lake trout older than age VII or VIII. Even in 1974–78, when lamprey predation was at the lowest level attained since sea lamprey control became effective in mid 1961, mortality due to lamprey predation L was greater than mortality due to fishing F and was roughly equal to normal natural mortality M. Since lake trout older than age VII or VIII now make up the bulk of the spawning stocks, sea lamprey predation severely restricts increases in spawning stocks needed for development of self-sustaining stocks.

The mortality that can be attributed to sea lamprey predation of lake trout younger than age VII or VIII in Lake Superior is unknown. Pycha and King (1975) presented some evidence that mortality is lower among the small fish than among the larger ones. Budd et al. (1969) showed reasonable evidence that L was nil for sizes below that at which lamprey marks were found, and increased with the incidence of lamprey marks. An assumption that seems reasonable is that L is almost nil among lake trout below the size and ages at recruitment (roughly 43 cm and ages IV–VI) and is no higher (probably lower) among the incompletely vulnerable sizes and ages than among the fully vulnerable older age-groups.

The only apparent management options are control of or reduction of sea lamprey abundance to control *L*, control of or reduction of fishing effort or the lake trout catch to control or reduce *F*, and stocking to maintain or increase recruitment. Since *L* is dependent on the predator–prey ratio (Lett et al. 1975), the effects of all of the above options are interdependent.

The estimated annual catch of lake trout in the study area in 1975–76 was roughly 409 000 kg (estimated from Table 2, with the assumption that average weight was about 1.8 kg). The 1975–76 average catch was about 65% of the 1929–43 prelamprey average catch and was about half the 1944–46 peak prelamprey catches in Michigan statistical districts 3, 4, and 5, which roughly correspond to the study area (Hile et al. 1951). Since *L* exceeded *F* in 1975–76, all the difference in annual yield between that in 1975–76 and that in 1929–46 can be accounted for by losses to sea lamprey predation. Total mortality rate *Z* estimated from the age distribution of catches in 11.4-cm-mesh gill nets in 1948 (Sakagawa and Pycha 1971) was lower than that in 1975–76, even though the fishery in 1948 was believed to have been operating at or slightly above the maximum equilibrium yield.

The evidence presented above suggests strongly that any management option that would increase the instantaneous rate of total mortality *Z* above the level in 1974–78 might prevent restoration of adequate spawning stocks and thus prevent attainment of the stated objective of lake trout rehabilitation. Prudent management should aim, at least, to prevent any increase in *Z*, and reduction of *Z* would be desirable.

If the sea lamprey could be eradicated, total catch held at the 1974–78 level, and recruitment maintained at the 1974–78 level by stocking, *L* would fall to nil and *Z* would decline by the amount of the reduction in *L*. The abundance of all sizes of lake trout vulnerable to sea lamprey predation would then increase within one growing season. With abundance increasing and total catch held constant, *F* would gradually decline; this decline, in turn, would cause a further reduction in *Z*. If the sea lamprey were reduced but not eradicated (other conditions remaining constant), *L* would be reduced but not eliminated, *F* and *Z* would be reduced, and the increase in abundance of all sizes of lake trout would be slower than with lampreys eradicated. Any increase in abundance of lake trout would decrease the predator–prey ratio and thus depress *L* by more than an amount directly proportional to the reduction of sea lampreys.

If control of sea lamprey abundance at the 1974–78 level were the maximum practical level of control, all fishing could be closed to reduce *F* to nil while recruitment was maintained at the 1974–78 level by stocking. The value of *Z* would then be reduced by the amount of reduction in *F*. Abundance of all vulnerable sizes of lake trout would increase and the increase in abundance of lake trout would reduce the predator–prey ratio; *L* in turn, would be somewhat reduced. Since *F* was less than *L* in 1974–78, closure of the fishery would have a less beneficial effect than would eradication of the sea lamprey.

If abundance of sea lampreys and the total catch of lake trout both remained at the 1974–78 level, *Z* could be reduced only by increased stocking. If recruitment were raised (by stocking) to double the 1974–78 level, abundance would double for one additional age-group each year. Total abundance would gradually approach double the 1974–78 level because of the increased stocking alone. Abundance of spawning stocks would eventually double, but the increased recruitment alone would not alter the age composition of spawning stocks. The increase in abundance would, however, reduce the predator–prey ratio to half the 1974–78 level; *L* should then be reduced substantially. The increase in abundance would also reduce the value of *F*. Reductions in *L* and *F* would reduce *Z* and increase survival which would increase the average age in the population. Eventually, the abundance of spawners would more than double and their average age would increase.

All of the management options have disadvantages. Eradication of the sea lamprey is a practical impossibility with present technology, and reducing the sea lamprey population below the 1974–78 level would almost certainly require increased expenditures. Closing fishing for lake trout would, at least temporarily, eliminate the principal tangible benefit of sea lamprey control. Increasing stocking rate could be the least unpleasant alternative, but all available hatchery capacity is now being used for stocking Lakes Superior, Michigan, and Huron. Thus, at present, the stocking rate in Lake Superior could be increased only if the rates in the other lakes were reduced. Even if sufficient hatchery capacity were available and the stocking rate were increased, the abundance of lake trout of sizes vulnerable to either the fishery or the sea lamprey would not increase for 3 to 4 years after the additional stocking began. The 1974–78 recruitment level resulted from the annual stocking of an average of 1.44 million yearling lake trout in the study area in 1966–70. After 1970 the stocking rate was reduced, and since 1972 the rate has been only about half the 1966–70 rate. Doubling the 1974–78 recruitment rate would require nearly quadrupling the 1973–78 stocking rate, even though the recruitment of native fish has increased.

Of the three management options possible, only one — reducing or eliminating the catch of lake trout — would act quickly to reduce *Z* and increase spawning stocks. Increasing the intensity of sea lamprey control would require time to obtain increased funding, time to apply the funds, and time for the parasitic-phase lampreys in the lake to mature and leave the lake. Increasing stocking could have no effect on *Z* for at least several years.

BUDD, J. C., F. E. J. FRY, AND P. S. M. PEARLSTONE. 1969. Final observations on the survival of planted lake trout in South Bay, Lake Huron. J. Fish. Res. Board Can. 26: 2413–2424.

ESCHMEYER, P. H. 1957. The near extinction of lake trout in Lake Michigan. Trans. Am. Fish. Soc. 85: 102–119.

FRY, F. E. J. 1953. The 1944 year class of lake trout in South Bay, Lake Huron. Trans. Am. Fish. Soc. 82: 178–192.

HILE, R., P. H. ESCHMEYER, AND G. F. LUNGER. 1951. Status of the lake trout fishery in Lake Superior. Trans. Am. Fish. Soc. 80: 278–312.

LAWRIE, A. H., AND W. MACCALLUM. 1980. On evaluating measures to rehabilitate lake trout (*Salvelinus namaycush*) of Lake Superior. Can. J. Fish. Aquat. Sci. 37: 2057–2062.

LETT, P. F., F. W. H. BEAMISH, AND G. J. FARMER. 1975. System simulation of the predatory activities of sea lampreys (*Petromyzon marinus*) on lake trout (*Salvelinus namaycush*). J. Fish. Res. Board Can. 32: 623–631.

PYCHA, R. L. 1970. Mortality rates of planted lake trout in Lake Superior. Great Lakes Fish. Comm. Rep. Interim Meet. Summary Minutes, App. III.

PYCHA, R. L., AND G. R. KING. 1975. Changes in the lake trout population of southern Lake Superior in relation to the fishery, the sea lamprey, and stocking, 1950–70. Great Lakes Fish. Comm. Tech. Rep. 28: 33 p.

RAHRER, J. F. 1967. Growth of lake trout in Lake Superior before the maximum abundance of sea lampreys. Trans. Am. Fish. Soc. 96: 268–277.

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

SAKAGAWA, G. T., AND R. L. PYCHA. 1971. Population biology of lake trout (*Salvelinus namaycush*) of Lake Superior before 1950. J. Fish. Res. Board Can. 28: 65–71.

Decline and Recovery of the Lake Superior Gull Island Reef Lake Trout (*Salvelinus namaycush*) Population and the Role of Sea Lamprey (*Petromyzon marinus*) Predation[1]

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The Gull Island Reef lake trout (*Salvelinus namaycush*) population was one of the few in Lake Superior that was not annihilated by the combined effects of excessive fishing and sea lamprey (*Petromyzon marinus*) predation. Following control of the lamprey in the early 1960s, this population of lake trout began a slow but steady increase in the average age and numbers of lake trout. Total annual mortality rates for spawning lake trout were 32% for age VI fish, 48% for ages VII–VIII, and 75% for ages IX and older. These total mortality rates included a 7.3% exploitation rate *u*, a 20% natural mortality *n*, and annual lamprey-induced mortalities of 6% for ages V–VI, 24% for ages VII–VIII, and 56% for ages IX and older fish. The estimated number of lake trout eggs deposited annually on Gull Island Reef from 1964 to 1979 ranged from 3.3 million eggs in 1965 to 28 million eggs in 1979, with a mean of 9 million eggs per year. At present levels of lamprey predation, the estimated egg to spawning fish return rate on Gull Island Reef is 0.18%.

Key words: lake trout, sea lamprey, survival, population structure, egg deposition

SWANSON, B. L., AND D. V. SWEDBERG. 1980. Decline and recovery of the Lake Superior Gull Island Reef lake trout (*Salvelinus namaycush*) population and the role of sea lamprey (*Petromyzon marinus*) predation. Can. J. Fish. Aquat. Sci. 37: 2074–2080.

La population de touladis (*Salvelinus namaycush*) du récif de l'île Gull est l'une des rares populations du lac Supérieur qui n'ait pas été annihilée sous les effets combinés d'une pêche intensive et de la prédation par la grande lamproie marine (*Petromyzon marinus*). À la suite du contrôle de la lamproie au début des années 1960, cette population de touladis commença, lentement mais régulièrement, à augmenter en âge moyen et en nombre. Les taux de mortalité totale annuelle des touladis reproducteurs étaient de 32% pour les poissons d'âge VI, 48% pour les âges VII–VIII et 75% pour les âges IX et plus. Ces taux de mortalité totale incluent un taux d'exploitation *u* de 7,3%, une mortalité naturelle *n* de 20% et des mortalités annuelles causées par la lamproie de 6% pour les âges V–VI, 24% pour les âges VII–VIII et 56% pour les âges IX et plus. Le nombre total estimé d'oeufs de touladi déposés annuellement sur le récif de l'île Gull entre 1964 et 1979 a varié de 3,3 millions d'oeufs en 1965 à 28 millions en 1979, la moyenne annuelle étant de 9 millions. Aux présents niveaux de prédation par la lamproie, le taux de retour des reproducteurs sur le récif de l'île Gull par rapport aux oeufs est de 0,18%.

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LAKE trout (*Salvelinus namaycush*) abundance in southern Lake Superior declined during the 1940s and early 1950s due mainly to excessive fishing. After this relatively gradual decline, the parasitic sea lamprey (*Petromyzon marinus*) ravaged the lake trout populations during the late 1950s and early 1960s (Pycha and King 1975). The damage to lake trout populations was especially apparent among the larger fish. The abundance of mature lake trout in the Apostle Islands area of Lake Superior was so low by 1962 that spawning activity had ceased at nearly all of the traditional spawning sites except on Gull Island Reef where a very small number of mature lake trout survived and continued to reproduce.

The combination of planting hatchery-reared fish in the late 1950s, controlling the lamprey in mid-1961, and restricting fishing in mid-1962 reversed the trend

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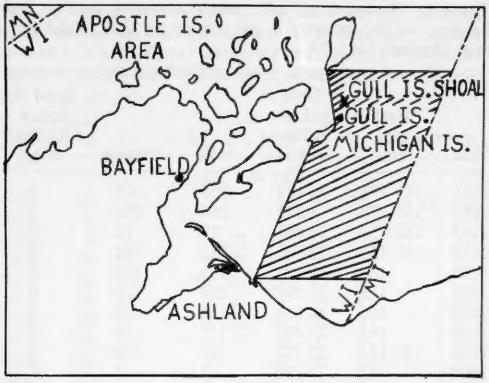

FIG. 1. Gull Island Reef area of the Apostle Islands Region, Wisconsin waters of Lake Superior. Shaded area is closed to lake trout fishing year around.

of declining lake trout abundance. Even though lake trout abundance had recovered substantially by 1970, spawning activity was not evident at most of the traditional spawning sites in the Apostle Island area. Recovery of the population on Gull Island Reef has been of considerable interest because it is one of the few in southern Lake Superior that recovered enough to sustain itself after the sea lamprey was brought under control.

Annual commercial lake trout harvests of 227 000 kg were common in Wisconsin waters of Lake Superior during the pre-lamprey years. In 1975–79 about 70 000 kg of lake trout, mostly hatchery-reared fish, were harvested annually. Even though the annual harvest of lake trout in Wisconsin waters of Lake Superior may never again reach pre-lamprey levels, the reestablishment of widespread natural reproduction could substantially increase the abundance of lake trout and reduce the need for stocking.

In this study we document the decline in the abundance and the subsequent recovery of the Gull Island Reef lake trout population once the lamprey was controlled, estimate mortalities of the lake trout spawning stocks due to predation by the residual lamprey population, illustrate changes in egg deposition in the years following effective sea lamprey control, and project future increases in the stocks.

Materials and Methods

The site for this study is a large (16 km long and 1.6–4.8 km wide) rocky reef located along the eastern edge of the Apostle Islands (Fig. 1). The reef is isolated from the other Apostle Islands on three sides by deep water (61–120 m) channels and exposed to the open lake on the fourth side. The three distinct rocky projections that extend upward from the reef are Michigan Island which is 4.8 × 1.6 km and rises 18 m above water; Gull Island which juts above the water's surface; and Gull Island Shoal with its apex 5.5 m underwater. Spawning condition lake trout have been captured each fall since 1952 in 5–60 m of water at various locations on the reef. Pre-1960 data were collected with 127–178 mm stretch-measure cotton or nylon gill nets fished by commercial fishermen that had contracted with the Wisconsin Department of Natural Resources to collect lake trout eggs and monitor lamprey wounding and scarring rates. Post-1960 data were collected by personnel from the Wisconsin Department of Natural Resources (DNR) and the U.S. Fish and Wildlife Service using 114–178 mm stretch measure gill nets. Fish were measured (total length), sexed, and examined for lamprey marks. Scales for aging were taken from most native and some of the hatchery-origin lake trout, pressed in acetate, and the images read at 80×. Difficulty in aging increased greatly with size and age of lake trout. Hatchery-reared fish were aged from their finclips when possible, but scales were used when fish stocked in different years bore the same clip. Scales from enough known-age fish were available to enable us to develop confidence in our age determinations.

Annual catches of native lake trout spawners on Gull Island Reef and catches of finclipped lake trout at five other locations in the Apostle Islands region were used to estimate mortality. Mortality rates of individual year-classes were estimated from the number of lake trout each year-class contributed to the total catch of 7- to 11-yr-old fish on the spawning grounds. Mortality estimates for the 6-yr-old lake trout were obtained by extending the mortality curves to include this age-group. High mortality due to an intensive commercial and sportfishery in 1975 reduced the population of lake trout spawners on Gull Island Reef by about 50% (Swanson 1976) but was limited to that one year because a 51 800 ha fish refuge was established in the Gull Island Reef area in early 1976 (Fig. 1). Creation of the refuge, which was closed to all lake trout fishing, reduced fishing mortality to about the 1974 level.

Estimates of the number of adult fish in the Gull Island Reef lake trout population were generated from a tag and recapture project in 1963–78. Tagging from 1963 to 1968 consisted of inserting a plastic poultry leg band around the fish's lower jaw, while the 1969–78 taggings were accomplished by inserting a plastic Floy dart tag through the apaxial muscle adjacent to the dorsal fin. Sloughing rates for the Floy tags were estimated from double tagging 1098 lake trout. Annual spawning population estimates were calculated by the Peterson method (Lagler 1956) which required that the following assumptions be satisfied:

1) Lake trout return to their natal reef to spawn (Eschmeyer et al. 1953; Eschmeyer 1955; Martin 1957; Loftus 1958; Rahrer 1968; and Swanson 1974). Tag returns from the Keweenaw Bay to Marquette area of Lake Superior revealed that most of the lake trout in that vicinity returned to specific localities for spawning, even though they dispersed widely between spawning seasons (Eschmeyer et al. 1953). Rahrer (1968) reported that all but one of the recaptured fish taken on Gull Island Reef during the 1962–65 spawning seasons had been tagged and released in that same area. Swanson (1974) reported that 98.6% of the recaptures during subsequent spawning seasons of lake trout tagged on Gull Island Reef in 1966–74 were taken on Gull Island Reef.

2) Lake trout, once mature, return to their natal reef each year to spawn. This assumption limits mortality estimates to male lake trout as the catch data on female lake trout suggests that not all of the females spawn every year. Recapture rates were higher for male lake trout than for

female lake trout the first year after tagging and similar for both sexes the second year after tagging. This indicates that some female fish did not return to the spawning grounds the first year after they were tagged. Cuerrier and Schultz (1957) reported that lake trout spawned every third year in Great Bear Lake, and every other year in Great Slave Lake and in the Watertown Lakes of Alberta. About 8% of the female lake trout in Lake La Ronge, Saskatchewan, Canada did not spawn in a given year. Rawson (1961), DeRoche (1966), and Royce (1951) believed that lake trout from Maine and New York spawned each year after they reached maturity.

3) Tag loss remained constant during the study period. Even though the Peterson population estimate works best when the recapture period is short, the circumstances involved with this study make a short recapture period impossible. The recapture period for this study was 1 yr after the fish were tagged. Since mortality increased with age, the number of lake trout available for recapture 1 yr after tagging was determined by dividing the tagged fish into three age-groups; ages VI, VII–VIII, and IX–XII+, and calculating survival for each.

Spring and fall lamprey wounding rates were determined from lake trout captured by fishermen fishing under contract to the Wisconsin DNR. Lamprey marks were considered wounds when no translucent slime or film covered the infliction; all others were considered scars.

Changes in the Lake Trout Population

ABUNDANCE

Catches of lake trout spawners on Gull Island Reef fluctuated during the 1950s and early 1960s from 55 fish per 1000 m of gill net in 1952, to only about 1 fish per 1000 m of gill net in 1960 (Table 1). Even though the conversion from cotton to nylon gill net in the early 1950s, and the addition of 114-mm mesh to the standard assessment gangs in the 1960s prevented us from using the annual catch data as an annually comparable index of relative lake trout abundance, the long-term trends in the 1952–79 catch data are roughly indicative of the changes that actually occurred. The decline in catches of lake trout spawners in 1952–60 represents a severe reduction in the abundance of spawning lake trout on Gull Island Reef. An initial gradual downward trend in abundance during the early 1950s was followed by a sharp decline beginning about 1956 (Pycha and King 1975). Wisconsin production of lake trout also declined severely during the late 1950s. Mortality rates of large lake trout must have been very high during the period before the sea lamprey was controlled because fish larger than 660 mm were scarce by 1961.

In 1962, after the onset of effective sea lamprey control and fishing restrictions, the number of lake trout spawners on Gull Island Reef began to increase. Effects of the lamprey control program were very evident by 1964 when catches of spawners increased substantially. Recruitment of native fish accounted for the increase in spawner abundance in 1962–64, while hatchery-origin lake trout accounted for most of the increase in 1965–70. Native lake trout were again responsible for the increase in the number of fish on Gull Island Reef during the 1970s.

TABLE 1. Numbers of lake trout spawners (native and hatchery origin) captured in gill nets set on Gull Island Reef each October, 1951–79.

Year	Mesh size (mm)	Total gill net fished (metres)	Male	Female	% of the catch hatchery origin
1951	165–178	16 159	363	167	0
1952	165–178	8 537	264	206	0
1953	152–191	16 463	59	78	0
1954	152–165	28 963	152	140	0
1955	165	18 293	253	206	0
1956	165	24 390	208	111	0
1957	165	14 634	134	38	0
1958	165	24 390	132	55	0
1959	127–165	32 317	197	30	0
1960	165	11 280	7	1	12
1961	127–165	10 610	5	0	0
1962	127–152	4 665	48	1	0
1963	114–152	18 384	34	5	2
1964	114–152	5 366	310	42	4
1965	114–152	5 457	341	41	7
1966	114–152	6 768	154	44	12
1967	114–152	7 134	149	59	26
1968	114–152	5 945	130	69	28
1969	114–152	5 945	125	37	25
1970	114–178	4 756	484	91	57
1971	114–178	4 756	461	94	30
1972	114–178	4 756	733	121	19
1973	114–178	4 756	413	112	29
1974	114–178	5 945	572	156	25
1975	114–178	4 756	261	118	28
1976	114–178	4 756	344	92	24
1977	114–178	4 756	658	79	18
1978	114–178	4 756	519	207	14
1979	114–178	4 756	684	389	12

AGE

Lake trout that utilized the Gull Island Reef spawning grounds during the pre-lamprey control 1950s were much older than those that spawned there during the post-lamprey control 1960s (Table 2). Thirty percent of the fish captured on Gull Island Reef during the 1957 spawning season exceeded age IX while no fish exceeded that age in 1962. This loss of older lake trout occurred while lamprey abundance was increasing. Older lake trout began to reappear shortly after lamprey control became effective. Gill net catches of age X lake trout increased from 1 in 1964 to 2 in 1965 and 15 in 1966 and the number of older lake trout caught increased each year thereafter. Increased catches of younger (ages V–IX) lake trout on the Gull Island Reef spawning grounds in 1962–79 was due largely to the addition of smaller-mesh nets in the standard assessment gangs rather than to an increase in the numbers of younger fish on the reef.

TABLE 2. Distribution of native lake trout spawners captured by gill nets in the Gull Island Reef, Lake Superior, October, 1957 and 1961–79. Data is expressed as percentage of fish aged.

Year	No. of fish aged	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
					Female lake trout						
1957	24						50	25	4	17	4
1961	0										
1962	3				33	34	33				
1963	30		3	7	30	60					
1964	74			4	45	38	12	1			
1965	74			4	41	35	19	1			
1966	96			5	20	49	18	8			
1967	116			1	17	52	27	3			
1968	123			1	7	57	28	7			
1969	61			3	16	41	30	10			
1970	85			2	11	47	27	9	4		
1971	92			5	18	27	19	17	4	7	3
1972	203			4	28	30	29	7	1	1	
1973	110				5	44	36	9	2	3	1
1974	291			1	22	43	24	8	1	1	
1975	155			3	12	43	29	10	2	1	
1976	144			1	19	48	24	8	1		
1977	106			1	9	34	30	21	2	2	1
1978	287			1	17	49	22	9	1	1	
1979	217		1	1	12	40	31	12	2	1	
					Male lake trout						
1957	28				18	36	32	7		4	3
1961	29		28	59	7	3	3				
1962	95	4	19	29	39	8	1				
1963	205		9	32	37	21	1				
1964	516		5	31	51	12	1				
1965	609		5	30	34	19	11	1			
1966	282			4	27	43	19	7			
1967	219			1	24	44	17	11	3		
1968	138			4	25	43	23	4	1		
1969	169		1	15	28	34	19	3			
1970	288		17	27	27	14	9	5	1		
1971	574		1	43	36	12	4	3	1		
1972	352		1	21	50	21	3	2	1	1	
1973	323		1	8	25	35	22	6	1	1	1
1974	1415		1	9	32	38	13	4	2	1	
1975	348		3	11	28	31	16	8	2	1	
1976	430		1	40	21	21	10	5	1	1	
1977	556		1	9	43	23	10	8	3	2	1
1978	686		3	6	28	44	13	3	1	2	
1979	383		7	23	16	23	18	9	2		2

POPULATION SIZE

The numbers of lake trout that spawned on Gull Island Reef each year from 1964 to 1979 were estimated to determine how rapidly that population recovered after the lamprey was controlled. The number of native males on the spawning reef ranged from 1291 ± 295 (95% confidence interval) in 1968 to 8635 ± 1316 in 1979 with a 15-yr mean of 4663 (Table 3). The 1964 and 1967 estimates are based on only 4 and 5 tag returns, respectively. The catches per unit effort for 1964 and 1967 suggest that the numbers of male spawners were lower in those years than their population estimates indicated. Abundance of native male lake trout in the Gull Island Reef population increased in 1964–65, 1971–74, and 1976–79, and decreased in 1966–70, and in 1975. The 1964–65 increase in abundance of spawners resulted from maturation of fish that were too young to be subject to sea lamprey predation during the years of high sea lamprey abundance. The 1966–70 decline in spawner abundance probably resulted from poor recruitment from the year-classes produced in 1956–62 when lamprey infestation was heaviest and abundance of spawners was low. The increases in the 1970s were the result of increases in the spawning population and natural reproduction in the 1960s and 1970s. The decrease in abundance in 1975 was caused by overfishing (Swanson 1976).

The numbers of native females, finclipped females, and finclipped males that utilized the Gull Island Reef spawning grounds in 1956–79 were estimated from the population estimates of mature native males, the sex ratio of the spawning stock, and the percentage of finclipped fish on the reef in each of those years.

Estimates of native females ranged from 430 fish in 1970 to 4508 fish in 1979, with a 15-yr mean of 1327 fish (Table 3). Possible differences in the behavior of male and female fish on the spawning reef might have affected the estimated number of female lake trout. However, Martin (1957) reported that both sexes of lake trout actively roam the spawning area in advance of spawning and we collected both male and female lake trout on Gull Island Reef just before they began to spawn. We assume that both male and female lake trout were caught in proportion to their abundance.

SEA LAMPREY WOUNDING AND SCARRING

The incidence of lamprey marks on lake trout was positively related to both the abundance of sea lampreys in Lake Superior (Smith et al. 1974) and to mortality rates of lake trout (Pycha and King 1975; Pycha 1980). Results of massive TFM (3-trifluoromethyl-4-nitrophenol) treatments of streams during the late 1950s and early 1960s were evident by 1962 when adult lamprey abundance had declined 80–90%. Lamprey marks (wounds and scars were not separated until 1960) on the Gull Island Reef lake trout increased from about 10% in the early 1950s to 90% in the late 1950s and in 1960–61 but declined to 50% in 1965, and to 35–40% in the late 1970s. In the spring of 1960, 33% of the large (>600 mm), 20% of the medium (400–600 mm), and 5% of the small (<400 mm) lake trout bore fresh lamprey wounds. By 1963, wounding rates had decreased to 2.3, 1.0, and 0.3% for the large, medium, and small lake trout, respectively. Since 1963, wounding rates have fluctuated slightly but systematic TFM treatments in the major lamprey producing streams have kept lamprey abundance relatively stable.

TABLE 3. Composition of the Gull Island Reef lake trout spawning population, 1964–79.

	Population estimate — natives only (±95% confidence interval)				Catch/300 m natives only			% hatchery origin		
Year	Males	No. of returns	Females	Total	Male	Female	Total	Male	Female	Both
1964	5553[a]	4	752	6 035	30.5	4.1	34.6	4.1	2.6	3.9
1965	5081±1029	20	628	5 709	31.7	3.9	35.6	5.8	5.4	5.6
1966	2748±495	24	858	3 606	12.6	3.9	16.5	16.6	2.3	12.3
1967	1735[a]	5	941	2 676	9.3	5.0	14.3	36.8	13.6	27.0
1968	1500±326	16	1267	2 767	7.6	6.4	14.0	41.0	13.3	28.5
1969	2709±674	13	997	3 706	7.3	2.9	10.2	39.5	26.2	35.1
1970	1580±395	4	430	2 010	19.6	5.1	24.7	58.6	43.6	56.6
1971	6299±1818	8	1138	7 437	31.6	5.7	37.3	28.8	39.6	30.2
1972	7642±1077	30	1213	8 855	57.9	9.2	67.1	18.8	22.5	19.4
1973	6477±1438	13	1470	7 946	28.6	8.2	36.8	26.8	39.2	29.0
1974	6069±748	36	1377	7 446	42.1	10.9	53.0	24.4	28.8	25.3
1975	(no estimate)				18.0	8.6	26.6	29.9	26.1	28.7
1976	3265±588	18	959	4 224	26.6	6.3	32.9	22.6	26.7	23.5
1977	4754±673	37	717	5 471	53.0	6.2	59.2	18.2	20.3	18.4
1978	5895±597	49	2648	8 543	43.2	18.1	61.3	15.9	12.3	14.8
1979	8635±1316	37	4508	13 143	42.2	22.0	64.2	11.3	10.9	11.1

[a]Based on CPE data.

Mortality–Age Relations

TOTAL MORTALITY

Total annual mortality rates *A* of native male spawners on Gull Island Reef ranged from 57% for 8- and 9-yr-old fish to 73% for 10- and 11-yr-olds (Table 4). The equation $Y = 31.06 + 10.56\,X$, where Y is annual mortality and X is age, describes the mortality rates of male lake trout from Table 4. Mortality estimates from the relation above by age-groups are:

VI–VII	32%
VII–VIII	43%
VIII–IX	53%
IX–X	64%
X–XI	75%
XI–XII	85%

TABLE 4. Lake trout annual total mortality estimates, Apostle Islands, Lake Superior, 1964–76.

	Age			
	VII–VIII	VIII–IX	IX–X	X–XI
Spring assessment finclips (Years of data)	40.3% (7)	58.9% (6)	74.8% (4)	—
Native male spawners 1964–69	Not all mature	54.8%	54.5%	70.0%
Native male spawners 1970–76	Not all mature	59.2%	65.9%	75.4%
All native male spawners 1964–76	Not all mature	57.0%	60.2%	72.7%
Unweighted mean	40.3%	57.6%	65.1%	72.7%

Substantial differences in mortality rates by age of lake trout necessitated dividing the fish into three groups. Values of *A* by age-groups of native male spawners were: 32% for age VI fish; 48% for ages VII–VIII fish; and 75% for ages IX–XII+ fish ($Z = 0.39$, 0.66, and 1.39, respectively).

FISHING MORTALITY

The rate of exploitation (u) was determined from tag recoveries and the estimated rates of tag retention and tag reporting. A return of 240 tags from 5431 tagged lake trout yielded an unadjusted estimate of $u = 4.4\%$. A special tag loss study (191 returns of 1098 double-tagged lake trout) produced tag retention estimates of 90% after 2 mo, 80% after 6 mo, 75% after 8 mo, and 65% after 1 yr. We selected the 25% tag loss estimate because most of the harvest by fishermen occurred 7–9 mo after tagging (May–July). A tag reporting rate of 80% (weighted average) was obtained by estimating the rates that the various user groups (commercial, native American, sport, and assessment) reported tags that they had recovered. Estimates of tag recoveries were based on examinations of commercial landings and creel census. An annual exploitation rate of 7.3% was calculated by applying the 25% tag loss and the 80% tag reporting rate adjustments to the 4.4% exploitation rate. Instantaneous fishing mortality rate F was determined from the relation $F = u\,z/A$ (Ricker 1975) and resulted in levels of F of 0.06 at age VI; 0.10 at ages VII–VIII; and 0.14 at ages IX and older.

NATURAL MORTALITY

Natural mortality *M* (including that caused by sea

TABLE 5. Subsequent survival and return to spawn — both sexes; survival in numbers, egg to age indicated. (Figures in parenthesis show survival rate from egg to age indicated.) (*Affected by 1975 heavy fishing mortality; **adjusting using CPE data.)

Spawning year	Total no. spawning females	Mean fecundity	Egg deposition	V	VI	VII	VII	IX	X	XI	XII+
1964	857**	5053	4 330 421	269	2765	4161	2914	1119	—	42	164
				(0.006)	(0.064)	(0.095)	(0.067)	(0.026)	(*)	(*)	(*)
1965	664	4936	3 277 504	63	1653	1693	2898	—	240	157	144
				(0.002)	(0.050)	(0.052)	(0.088)	(*)	(*)	(*)	(*)
1966	878**	5875	5 158 250	76	518	2245	—	557	531	85	219
				(0.001)	(0.010)	(0.043)	(*)	(*)	(*)	(*)	(*)
1967	1089	5648	6 150 672	65	560	—	1145	690	415	263	
				(0.001)	(0.009)	(*)	(*)	(*)	(*)	(*)	
1968	1461	5756	8 409 516	61	—	868	1337	1348	1318		
				(0.0007)	(*)	(*)	(*)	(*)	(*)		
1969	1351	6117	8 264 067	—	1315	2108	3892	2951			
				(*)	(*)	(*)	(*)	(*)			
1970	762	5631	4 290 822	33	435	2101	3789				
				(0.0008)	(0.010)	(0.048)	(0.088)				
1971	1884	5775	10 880 100	48	380	1923					
				(0.0004)	(0.003)	(0.018)					
1972	1565	4942	7 734 230	177	2031						
				(0.002)	(0.026)						
1973	2417	4840	11 698 280	649							
				(0.005)							
1974	1934	5072	9 809 248								
1975	1173**	5518	6 472 614								
1976	1306	5982	7 812 492								
1977	916	5950	5 450 200								
1978	3019	5341	16 124 479								
1979	5052	5570	28 139 640								
Mean survival rate (excluding heavy fishing years)				0.0021	0.0246	0.0320	0.0810	0.0260			
(No. sample years)				(9)	(7)	(5)	(3)	(1)			
Mean survival rate (including heavy fishing years)				0.0021	0.0235	0.0420	0.0540	0.0200	0.0100	0.0030	0.0040
(No. sample years)				(9)	(8)	(7)	(6)	(5)	(4)	(4)	(3)

lampreys) accounted for most of the total mortality of lake trout in the Gull Island Reef area for all years except 1975 when fishing mortality was exceptionally high. Sakagawa and Pycha (1971) estimated the mean rate of instantaneous natural mortality *M* for age IX and older lake trout in Lake Superior as 0.22 during the pre-lamprey years. We subtracted Sakagawa's and Pycha's natural mortality rate (0.22) and our fishing mortality *F* from the instantaneous rate of total mortality *Z* for the three age groups of lake trout spawners to obtain an estimate of the instantaneous rate of lamprey-caused mortality *L*. *L* was estimated at 0.08 for age VI spawners, 0.33 for age VII–VIII spawners, and 1.03 for ages IX and older spawners (these rates correspond to annual losses to lamprey of 6.5, 24, and 55.6%, respectively).

Egg Deposition and Survival

Lamprey predation is still the largest single source of mortality of age VII and older lake trout on Gull Island Reef and lamprey control is, therefore, a requisite for adequate egg deposition. Egg depositions for the pre-lamprey control and first few post-lamprey control years are not known but we can reasonably assume from the small numbers of females collected on Gull Island Reef in 1957–63 that egg depositions were low during those years. Annual egg depositions, calculated from fecundity estimates (Eschmeyer 1964) and annual estimates of female fish on Gull Island Reef, ranged from 3.3 million in 1965 to 28 million in 1979.

We calculated an egg to spawning fish return rate for lake trout subjected to postcontrol levels of lamprey predation from the number of eggs deposited each year and the subsequent number of spawnings that resulted from those eggs (Table 5). Total spawnings of each year-class were obtained by summing the annual spawnings of members of that year-class at all ages. The total obtained by this procedure exceeded the egg to mature fish survival rate because fish were counted every time they spawned. The estimated egg to spawning fish return rate which varied considerably from year-to-year totaled 0.17% (age V–IX) when the data affected by the high 1975 fishing mortality were excluded. A slightly lower 0.16% (age V–XII) return rate resulted when the ages affected by the high 1975 mortality were included. A total return rate of 0.18% was obtained by adding the rates for the years not affected by the 1975 mortality (age V–IX) to the rates for age X and older fish that were affected by the 1975 mortality.

If present trends continue and lamprey abundance remains stable, we estimate that 19–20 million eggs will be deposited on Gull Island Reef in 1981. These eggs should produce a return of about 35 000 spawnings during the late 1980s and early 1990s or more than double the number of spawnings that occurred on Gull Island Reef during the late 1970s.

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Cuerrier, J. P., and F. H. Schultz. 1957. Studies of lake trout and common whitefish in Watertown Lakes, Watertown Lakes National Park, Alberta. Can. Wildl. Serv. Wildl. Manage. Bull. 3: 41 p.

DeRoche, S. F. 1966. Lake trout *Salvelinus namaycush* (Walbaum), p. 42–45. *In* W. H. Everhart [ed.] Fishes of Maine. 3rd ed. Maine Dep. Inland Fish. Game, ME.

Eschmeyer, P. H. 1955. The reproduction of lake trout in southern Lake Superior. Trans. Am. Fish. Soc. 84: 47–74.

1964. The lake trout (*Salvelinus namaycush*). U.S. Fish Wildl. Serv. Fish. Leafl. 555: 8 p.

Eschmeyer, P. H., R. Daly, and L. F. Erkkila. 1953. The movement of tagged lake trout in Lake Superior, 1950–52. Trans. Am. Fish. Soc. 82: 68–74.

Lagler, K. F. 1956. Freshwater fishery biology. Wm. C. Brown Co., Dubuque, IA. 421 p.

Loftus, K. H. 1958. Studies on river-spawning populations of lake trout in eastern Lake Superior. Trans. Am. Fish. Soc. 87: 259–277.

Martin, N. V. 1957. Reproduction of lake trout in Algonquin Park, Ontario. Trans. Am. Fish. Soc. 86: 231–244.

Pycha, R. L. 1980. Changes in mortality of lake trout (*Salvelinus namaycush*) in Michigan waters of Lake Superior in relation to sea lamprey (*Petromyzon marinus*) predation, 1968–78. Can. J. Fish. Aquat. Sci. 37: 2063–2073.

Pycha, R. L., and G. R. King. 1975. Changes in the lake trout population of southern Lake Superior in relation to the fishery, the sea lamprey, and stocking, 1950–70. Great Lakes Fish. Comm. Tech. Rep. 23: 34 p.

Rahrer, J. F. 1968. Movements of adult lake trout in Lake Superior. Trans. Am. Fish. Soc. 97: 481–484.

Rawson, D. S. 1961. The lake trout of Lac La Ronge, Saskatchewan. J. Fish. Res. Board Can. 18: 423–62.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

Royce, W. F. 1951. Breeding habits of lake trout in New York. U.S. Fish. Wildl. Serv. Fish. Bull. 52: 59–76.

Sakagawa, G. T., and R. L. Pycha. 1971. Population biology of lake trout (*Salvelinus namaycush*) of Lake Superior before 1950. J. Fish. Res. Board Can. 28: 65–71.

Swanson, B. L. 1974. Lake trout homing, migration, and mortality studies, Lake Superior. Wisc. Dep. Nat. Res. Manage. Rep. 65: 22 p.

1976. Depletion of Gull-Michigan Island native lake trout spawning population. Lake Superior stock assessment report, Wis. Dep. Nat. Res. 5 p.

Smith, B. R., J. J. Tibbles, and B. G. H. Johnson. 1974. Control of the sea lamprey (*Petromyzon marinus*) in Lake Superior, 1953–70. Great Lakes Fish. Comm. Tech. Rep. 26: 60 p.

Prospects for Integrated Pest Management of the Sea Lamprey (*Petromyzon marinus*)[1]

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SAWYER, A. J. 1980. Prospects for integrated pest management of the sea lamprey (*Petromyzon marinus*). Can. J. Fish. Aquat. Sci. 37: 2081–2092.

The concepts of integrated pest management (IPM) may be applied to the problem of controlling the sea lamprey, *Petromyzon marinus*, in the Great Lakes. IPM originated as the integration of biological and chemical methods of insect control. It has since evolved into an interdisciplinary approach to ecologically, economically, and socially compatible pest control based on applied systems ecology, real-time monitoring systems and optimal control theory. The component processes of sea lamprey population dynamics are discussed with reference to key ecological variables and possible control points. To implement an integrated approach to sea lamprey pest management successfully, work is needed on basic lamprey biology and ecology, predictive models, alternative control tactics, and the economics of lamprey-induced injury to fish.

Key words: Petromyzon marinus, sea lamprey; integrated pest management, systems analysis, modeling

SAWYER, A. J. 1980. Prospects for integrated pest management of the sea lamprey (*Petromyzon marinus*). Can. J. Fish. Aquat. Sci. 37: 2081–2092.

Les principes de la gestion intégrée des pestes (IPM, « integrated pest management ») peuvent s'appliquer au contrôle de la grande lamproie marine, *Petromyzon marinus*, dans les Grands Lacs. L'IPM a commencé comme intégration des méthodes biologiques et chimiques de contrôle des insectes. Elle a évolué depuis en une approche interdisciplinaire d'un contrôle des pestes écologiquement, économiquement et socialement conciliable, fondée sur l'écologie des systèmes appliqués, sur les systèmes de contrôle en temps réel et sur la théorie du contrôle optimal. L'auteur analyse les processus des divers éléments de la dynamique des populations de grandes lamproies marines en relation avec des variables écologiques clés et des points de contrôle possibles. Si l'on veut appliquer avec succès l'approche intégrée à la gestion de la grande lamproie marine, il faudra étudier la biologie et l'écologie de base de l'espèce, les modèles prévisionnels, les autres tactiques de contrôle et l'économique des dommages causés aux poissons par la lamproie.

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THE purpose of this paper is to outline the principles of integrated pest management (IPM) and to discuss the prospects for applying its concepts and tactics to the problem of managing the sea lamprey, *Petromyzon marinus*, in the Great Lakes.

It is often stated, somewhat critically, that there are as many definitions of IPM as there are workers in the field (e.g. Mills 1978). IPMs beginnings in various traditional crop protection methods, its rapid conceptual and technical evolution in recent years and its interdisciplinary nature, as well as a recent increase in the number of participating workers (and the rapidly expanding awareness and expectations of many of them) have all contributed to this confusion. There are occasional claims that IPM is what economic entomologists have been practicing for decades. While many of its component tactics have, indeed, been used throughout the 20th century, it is only in recent years that IPM has emerged as a structured discipline with a coherent philosophical basis (Giese et al. 1975).

While originally concerned with insect pests of agriculture, IPM now considers the full spectrum of crop protection from arthropod, disease, weed, nematode, and vertebrate pests. Indeed, the principles of integrated pest management are applicable to a much broader range of environmental management problems (Watt 1968; Koenig 1974; Koenig et al. 1976). The approach is essentially one of applied systems ecology. It should be useful in almost any situation in which a complex natural or seminatural system is to be managed by manipulating biological and abiotic factors that are controllable and monitoring those that are not, and in which our understanding of the system's behavior can be represented by predictive models. Pest control is a special case in this class of problems, and may ulti-

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mately be arrived at simply as a consequence of comprehensive resource management (Geier and Clark 1960). There is, therefore, a potential for applying the IPM approach to the sea lamprey problem. There are enough differences between crop production systems and fisheries, however, to make the problem a challenging one. Some of these possibilities and limitations will be discussed in this paper.

The biases of an entomological viewpoint will undoubtedly flavor many of the statements and arguments in this paper. But this must be accepted as a hazard of breaching disciplinary boundaries — a necessity in any consideration of contemporary IPM.

Principles of Integrated Pest Management

MOTIVATION AND EARLY CONCEPTS

Koenig et al. (1976) described the classical approach to pest control as one in which a problem is first identified, one or more independent, discipline-oriented lines of research on control methods are followed, and the most promising of these methods are then recommended. Failure to achieve control is followed by a reevaluation of alternatives and continued research. This approach to pest control reached its height with the development and proliferation, following World War II, of the broad spectrum organic pesticides. During the optimistic early years of chemical control, in which success was initially very high, much less attention was paid to basic pest biology and to cultural and biological methods of pest control.

Very serious problems with this unilateral, chemical approach to pest control soon became apparent (NAS 1969; Doutt and Smith 1971). These problems included: (1) selection for resistant pest populations, (2) rapid appearance of cross resistance to substitute chemicals, (3) rapid resurgence of treated populations, (4) development of secondary pest problems in which nonpests became pests and minor pests became major pests, (5) undesirable effects on nontarget organisms, (6) residues, hazards and the associated legal complications, (7) increased costs of crop production, and (8) the still largely unassessed consequences of general environmental contamination with poorly understood synthetic organic chemicals.

These problems were, and still are, the primary motivating force for the formation of new attitudes and approaches to pest control. The term *integrated control*, appearing in 1956, was initially used to mean the use of pesticides in ways which would complement, rather than interfere with, biological control (Bartlett 1956; Stern et al. 1959). In addition to the integration of chemical and biological controls, two other important principles distinguished early approaches to pest management (Stern et al. 1959; Geier and Clark 1960). First, the need to establish an ecological basis for pest control was recognized. This meant that the natural factors regulating pest populations must be understood, conserved, and manipulated, and that control measures must be selective, and based on sampling and prediction rather than on preventative, "insurance" treatments. Geier and Clark (1960) argued that from an ecological viewpoint we should think in terms of "protective population management" rather than pest control. Second, the concept of the economic threshold was developed and became the basis for making control decisions. Stern et al. (1959) defined the *economic injury level* as "the lowest population density that will cause economic damage." When the pest population is below the economic injury level, the cost of applying artifical control measures would be greater than the benefits obtained. The *economic threshold* is a lower density, at which a decision to take action must be made to prevent an increasing pest population from exceeding the economic injury level before controls can be applied and take effect.

MODERN CONCEPTS OF IPM

During the late 1960s and 1970s the concept of pest management quickly evolved, largely as a result of advancing technology and increasing awareness of the broad applicability of the approach. The term *pest management* was suggested as being more descriptive of the philosophy than was *integrated control* (NAS 1969), and, in recent years, the designation *integrated pest management*, or IPM, has come to predominate (Glass 1975; EPA 1978). The significance of the term *integrated* in modern usage is at least three-fold (NAS 1969; Glass 1975; Luckmann and Metcalf 1975). First, it calls for a transdisciplinary viewpoint in which all classes of pests and their interrelationships are jointly considered, and in which crop protection is seen as contributing to the overall management of an agroecosystem. Second, it extends the early concept of integrated control as the combination of chemical and biological control to the integration of *all* available management techniques. This does not merely imply the simultaneous but independent application of two or more control methods, but rather their coordination into a unified program which seeks the optimal control. The analytical tools needed for this synthesis, such as electronic digital computers, systems analysis, and optimal control theory, have only become available to the applied biologist within the last 10–20 yr (Dale 1970; Davis 1977; ESC 1974; Garfinkel 1962; Haynes 1971; King and Paulik 1967; Shoemaker 1973; Varadarajan 1979; Watt 1961a, b, 1966). Finally, IPM recognizes the need for the integration of economic, ecological, and social concerns.

More than a collection of control techniques, IPM is perhaps most essentially a philosophical viewpoint, or an attitudinal approach to pest problems. The philosophy incorporates the following principles:

1) Pest problems must be approached from an ecological viewpoint. The natural factors regulating pest populations must be understood and managed to our benefit.

2) The need for artificial control measures should be determined on the basis of quantitative sampling, prediction of population trends, and economic thresholds.

3) Pest populations should be maintained at a maximum level below the economic threshold. Such a strategy is, by definition, economically acceptable. It also minimizes pesticide use, minimizes the disruption of natural enemy populations, reduces the selective force for the development of pesticide resistance, makes the greatest use of density dependent regulation and may result in lower control costs (Geier and Clark 1960; NAS 1969).

4) Pesticides are an important management tool, but because of their typically disruptive influence, they should be used as a last resort, only when really needed and then as selectively as possible (Doutt and Smith 1971; Luckmann and Metcalf 1975; Huffaker et al. 1976).

5) The concepts of eradication and preventative treatments are antithetical to a philosophy of pest management as outlined here (NAS 1969; Huffaker et al. 1976).

TECHNIQUES AND TOOLS OF IPM

A number of pest control methods have long been in use. Others are of more recent origin or are in various stages of development and evaluation (NAS 1969; Glass 1975; Metcalf and Luckmann 1975; Smith and Pimentel 1978). The general types of controls are: (1) host resistance, (2) biological control, (3) chemical control, (4) physical control, (5) cultural manipulations, (6) genetic techniques, and (7) selective behaviorally and physiologically active chemicals such as attractants, repellants, feeding deterrents, antimetabolites, hormones, and pheromones.

What characterizes IPM as a new approach to pest control is the integration of these tactics in ways which "ensure favorable economic, ecological and sociological consequences" (Luckmann and Metcalf 1975). As Haynes (1971) has said, however, "the complexity of problems associated with the terms 'pest management' is frightening to the uninitiated or to anyone who tries to look at the whole problem with all its interactions at one time." A major breakthrough in the field of pest management came with the realization that by viewing the problem in the context of systems analysis, the complexities of understanding and managing an agroecosystem could be handled rationally and quantitatively.

The general goals and philosophical approach of systems ecology and many examples of its application to natural and managed ecosystems are discussed in some detail by Arnold and deWit (1976), Hall and Day (1977), Jeffers (1978), Patten (1971-76), Shugart and O'Neill (1979) and Watt (1962, 1966, 1968).

Integrated pest management, as a special case of resource management, has proven to be a problem area to which the systems approach can be profitably applied. Barr et al. (1973), ESC (1974), Haynes (1971) and Koenig et al. (1976) provide a framework for viewing IPM in the context of systems analysis. IPM has been formulated as an on-line control problem by Giese et al. (1975), Haynes et al. (1973) and Tummala and Haynes (1977).

Central to any pest management system are quantitative predictive models representing our understanding of the dynamics of the pest population. Ruesink (1975, 1976), Shoemaker (1977), Tummala et al. (1976) and Watt (1961b) provide overviews of the development of models for use in pest management. In general, models play important roles in the analysis, management and design of agroecosystems.

In a research, or analytical mode, models are generally detailed descriptions of the structure and function of the real system. The modeling exercise helps in organizing existing knowledge and expressing relationships formally, logically and quantitatively. This quickly leads to the identification of missing or inadequate information, and thus helps to guide future research. Modeling makes it easier to deal with the complexity of an agroecosystem by identifying separate component processes and their interactions. This "allows each entomologist the freedom to work on small manageable aspects of the problem and still have confidence that his work will be positive input toward the solution to our ultimate goal of pest control" (Haynes 1971). Models may be used to explore the general behavior of the system and its response to specific conditions and stimuli, and contribute to the generation of testable hypotheses. Experiments which would be difficult or impossible to perform on the real system may be evaluated using a model of the system.

As management tools, predictive models may range from simple phenological models which forecast the occurrence of events to more detailed quantitative models which also provide predictions of pest population levels, damage, yield, etc. (Welch et al. 1978). Management models may be used to evaluate alternate control measures, make economic analyses of management options, and provide recommendations which take into account the dynamic interactions of pest populations and the crop environment. Optimization techniques can be used with mathematical models to determine the best management program (Clark 1976; Shoemaker 1973; Varadarajan 1979). Sensitivity analyses may identify key management factors.

The research and management functions of models may be combined to aid in the design of new systems. Here, the actual structure of the system is altered by introducing new crop varieties, natural enemy species, management tools, etc. Models can be invaluable in identifying alternate system designs which might improve pest control (Tummala et al. 1978).

Figure 1 depicts the structure of an operational pest management system based on predictive models (Koenig et al. 1976). Real-time environmental and

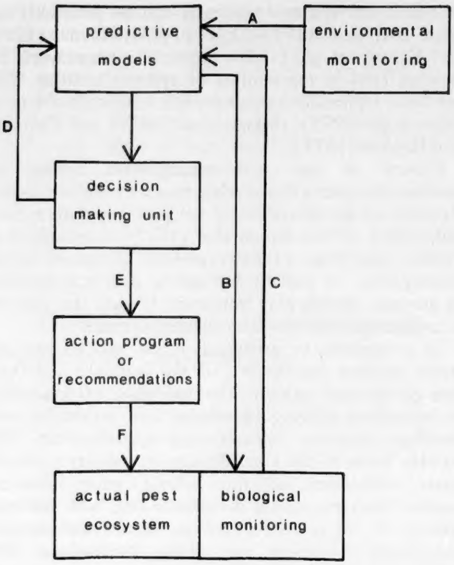

FIG. 1. Components of an operational pest management system (from Koenig et al. 1976).

biological monitoring networks and a high-speed communications facility are other important components of the system (Haynes et al. 1973; Giese et al. 1975). Environmental factors strongly influence ecosystem processes. Where these factors are unpredictable they must be monitored closely to provide the information needed to update the models. Biological monitoring provides models with initial estimates of pest density, crop conditions and other ecological states. It also provides for the important condition of closed-loop, or online control.

The principles of *on-line pest management* have recently been set forth by Tummala and Haynes (1977). In an on-line system, the components of Fig. 1 are used to implement strategies which are "continuously reviewed in light of changing meteorlogical conditions, the ecological state of the ecosystem, and the relative effectiveness of previous control strategies." Biological monitoring "closes the loop," providing information on the response of the ecosystem to control actions and serving to keep the model synchronized with events as they occur in the field. The need for on-line control arises from the fact that the predictive models are, after all, simple abstractions of the ecosystem, and many of the model's parameters and inputs vary stochastically. Thus while short-term predictions may be accurate, the models will deviate from reality in the long run without frequent updating. As our level of understanding of the ecosystem increases and new data are incorporated into the models, the dependency on frequent monitoring decreases.

In agricultural situations often only very short time lags in the various communications links (A–F) may be acceptable. For example, because of rapidly changing conditions in the field, control recommendations must be transmitted and carried out quickly (links E and F) once a need for action is determined, to prevent the pest population from exceeding the economic injury level. This had led to the development of computer-based pest management information systems (Croft et al. 1976; Haynes and Tummala 1978) and automated weather networks (Giese et al. 1975, Haynes et al. 1973). Time lags may be shortened still further by using anticipatory, *feed-forward* control as well as adaptive, feedback control. With this approach management steps are undertaken on the basis of the *anticipated* response of the ecosystem to control actions and environmental variables, as well as on the perceived response of the ecosystem to previous strategies and conditions.

LIMITATIONS TO IMPLEMENTATION

The factors most limiting to the immediate implementation of pest management systems in agriculture today are: (1) insufficient biological information about many of the agroecosystems, (2) a lack of data which will lead to the establishment of economic injury levels, (3) a lack of clearly stated, compatible objectives for IPM programs, and (4) disciplinary roadblocks.

The biological information needed to construct pest ecosystem models will come with research dedicated to filling this need. The data must be quantitative, and will be most efficiently obtained and useful if the research is guided by preliminary modeling efforts. The research/modeling process should be an iterative one, as modeling guides research and research facilitates modeling.

Economic injury levels have been difficult to establish because of the many factors affecting the interaction between a pest population and the resource to be protected. The original concept of the economic injury level was based simply on a critical population density, although it was recognized that this critical density varied from year to year and from region to region (Stern et al. 1959). It is now recognized that such factors as the age distribution of the pest population, the physiological state of the crop, weather conditions, natural enemy populations, and economic variables all affect the impact of a given pest density. The concept of the *dynamic damage threshold* (Giese et al. 1975) or *multidimensional economic threshold* (Shoemaker 1976) is an important advance in this regard. Such thresholds are difficult to establish empirically, however. Mathematical models may aid the process by synthesizing what is understood about the behavior of the crop ecosystem. Analysis or simulation may then yield predictions of the economic consequences of any particular set of ecological conditions and pest control actions (Shoemaker 1977).

There are many reasons for wishing to implement integrated pest management systems. Unfortunately, the several possible goals are not always compatible. The objectives of pest management may include: (1) higher yields and product quality, (2) lower production costs, (3) reduced pesticide usage and (4) the maintenance of ecological stability within the agroecosystem, among others. However, it is an established fact that "it is not mathematically possible to maximize for two (or more) variables at the same time" (Hardin 1968). A solution to this problem is to combine several variables, or goals, into a single objective function which is then maximized by the techniques of optimal control theory (Clark 1976; Shoemaker 1973; Varadarajan 1979). All components of the objective function must be expressed in terms of the same units, such as dollars or energy value. Herein lies another problem: certain objectives may seem to be incommensurable. Can the yield of a crop be expressed in the same terms as ecological stability or the impact of a pesticide on nontarget organisms? Hardin (1968) claims that "in real life incommensurables *are* commensurable. Only a criterion of judgement and a system of weighting are needed. The problem for the years ahead is to work out an acceptable theory of weighting." The solution to this problem is vital to the philosophical and practical viability of pest management. When the several objectives are placed in economic terms, the problem of optimizing the objective function becomes synonymous with the problem of maintaining the pest population at the multidimensional economic injury level.

Another limitation to the successful application of optimal control theory to pest management has been the upper limit on the number of state variables, or descriptors of conditions in the agroecosystem, which may be considered at once. This number has typically been limited to 3 or 4, placing severe constraints on the realism of the resulting models. Recently Varadarajan (1979) has been able to apply new techniques to the optimization of simulation models, increasing the allowable complexity of the models dramatically.

The successful development and implementation of modern pest management systems depend on the cooperation and interaction of research and extension people from a wide variety of disciplines, and an ability on the part of the effort's leaders to take a transdisciplinary, or all-encompassing, viewpoint. Traditional institutional structures and a general lack of professional incentives for crossing disciplinary boundaries hinder such activity. Since 1972, federal monies for agricultural IPM have been made available and this has encouraged interdisciplinary work (Huffaker 1978).

Integrated Pest Management of the Sea Lamprey

The objectives of pest management may seem, at first glance, to be entirely different from those of fisheries management: pest control seeks to minimize a population's size and limit its rate of increase, while fisheries seek to maximize the harvestable portion of a population while maintaining its reproductive potential. The problem is really the same, however: to manipulate natural and artificial mortalities in order to regulate a population's dynamics to our benefit. In the broader context of crop protection, pest management seeks to optimize the harvest of a crop within economic, ecological, and social constraints. This is exactly the goal of fisheries management (Clark 1976), and the regulation of pests such as the sea lamprey is simply a component part of the process.

Because of the economics peculiar to the exploitation of a common property resource (Hardin 1968; Clark 1973, 1976), and the difficulty of controlling environmental and biological factors in large bodies of water, the primary management tool of fisheries has been the regulation of harvesting rates and procedures (Cushing 1975; Gulland 1974, 1977; Johnson 1959; Rounsefell 1975). Other management tools are certainly available, however, such as breeding, stocking and removal of species, the use of barriers and shelters, the alteration of substrate materials, provision of food organisms, vegetation control, fertilization, and the management of such environmental parameters as temperature and oxygen (Paulik 1969; Rounsefell 1975; Royce 1972). These kinds of manipulations are heavily relied upon in aquaculture and mariculture (Bell 1978; Stickney 1979), lake rehabilitation efforts, and for the improvement of trout streams (Usinger 1971). An outstanding example of the use of stocking is the attempt to restructure the fish community of the Great Lakes by introducing new predatory species (Paulik 1969; Smith 1968). Additional nonregulatory techniques will be discussed below with reference to their possible use in the management of the sea lamprey.

Many of the techniques of modern IPM are not new to the management of fisheries resources: in fact, fisheries has provided important leadership in certain areas. For example, because of the early needs for reasonably precise quantitative methods, fisheries has been in the forefront of developments in theoretical and applied population dynamics (Gulland 1977). The problems of assessing abundance, age structure, reproduction, development, survival, dispersal, and the impact of human activities on populations were addressed in detail by Baranov (1918), Beverton and Holt (1957), Ricker (1948), Watt (1955, 1959), and other early workers in fisheries research. Mathematical and computer simulation models have been applied to fisheries problems for years, and their potential for future use seems to be increasing (Beyer and Laurence 1980; Clark 1976; Cushing 1975; Deangelis et al. 1980; Gulland 1969, 1977; Larkin 1971; Lett et al. 1975; Park et al. 1974; Paulik 1969; Ricker 1977; Silliman 1967, 1969; Steele 1977; Van Winkle 1977; Walters 1969, 1980; Watt 1955, 1967; Yeh and Yeh 1980). The need for environmental monitoring and on-line management systems for fisheries resources has been

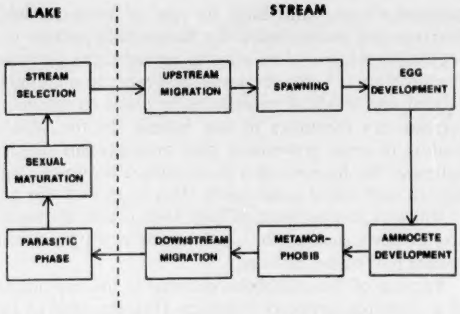

FIG. 2. Component processes of sea lamprey population dynamics.

recognized by some workers (Regier 1977; Paulik 1969), particularly where the resource is variable and responsive to weather phenomena. The economic aspects of fisheries management are particularly well developed (Clark 1976).

The application of IPM to the sea lamprey problem is discussed by reference to Fig. 2, a functional block diagram of sea lamprey population dynamics. Each box represents a biological process involving time delays and incorporating population loss factors. These losses may be due to natural mortality, artificial control measures, reduced fecundity, etc. Ideally each process is understood and can be quantitatively described and modelled, perhaps in terms of more detailed submodels (Ruesink 1975; Tummala et al. 1975). For each process some critical ecological variables, potential control points, relevant literature and needed research areas will be indicated. This will be followed by a general discussion of the prospects for applying the principles and procedures of IPM to the problem of sea lamprey control.

The period of upstream movement of adult lampreys was identified by Applegate (1950) as one of the times that control measures might be most effectively applied against the species, as the entire adult population is confined to the streams for a relatively short period. Mechanical and electrical barriers have been used in attempts to block upstream migration (Smith 1971), but with the development of chemical lampricides, research on physical control methods declined. Recent interest in integrated controls has stimulated renewed investigations on barrier dams, obstructions and velocity barriers (Hunn and Youngs 1980). The energy demands of upstream movement may be a factor affecting fecundity and prespawning mortality (Larsen 1980). The length of the upstream migratory period, and hence the energy requirements and survival probability for this period, are probably related to stream temperature and velocity, sky conditions, and the distance to the spawning grounds. Little is known about these factors. Predation may impose additional mortality at this time, but lampreys seem to have few natural enemies (Applegate 1950).

An understanding of spawning behavior is important to the development of several alternative control measures (Manion and Hanson 1980). Nest sites are selected which provide specific environmental conditions: suitable water temperature, a substrate consisting of gravel with some sand, and a unidirectional current (Applegate 1950). Any manipulations altering these conditions might reduce nesting success. Intra- and interspecific competition for nest sites and direct interference under crowded conditions are potentially important compensatory mortality factors (Applegate 1950; Ricker 1977). The sterile-male technique (Hanson and Manion 1978, 1980) depends on monogamous or polygynous mating behavior, and competitiveness of sterilized males with untreated males in nest building and spawning activities. The use of the chemosterilant, bisazir (*P*, *P*-bis(1-aziridinyl)-*N*-methylphosphinothioic amide), in the sterile-male approach should be viewed with caution. Chemosterilants are in general highly mutagenic and carcinogenic, and for this reason Metcalf and Metcalf (1975) recommended that they not be used in pest management programs. The possibility that bisazir injected into lampreys intraperitoneally may subsequently be excreted into the environment (Hanson and Manion 1980) should be a cause for concern. The sterile-male technique is often associated with the concept of eradication (Hanson and Manion 1980), which, in general, is not a goal of IPM (NAS 1969; Huffaker et al. 1976), but the application of the technique need not be limited to that extreme. Where the economic injury level is low in comparison to the pest population's general equilibrium point (Stern et al. 1959), the sterile-male technique may be an efficient means of maintaining an acceptably low pest density (Metcalf and Metcalf 1975). Other genetic control techniques involving the selective inheritance of lethal or deleterious genes should also be given consideration (NAS 1969). Pheromones, attractants and repellents capable of disrupting the spawning process might potentially be used in a management program (Metcalf and Metcalf 1975; Teeter 1980).

The high reproductive potential of spawning females is apparently never realized. A varying percentage of eggs are not extruded. Many eggs may fail to be deposited or retained in the nest due to the effects of water currents, inferior nest materials, and disruption of the nest by adult activities. The survival of eggs lost from the nest is probably low, but survival within the nest is high (Manion and Hanson 1980). The developmental rate of eggs is a function of water temperature which may vary considerably in spawning streams (G. W. Piavis School of Dentistry, Univ. Maryland, Baltimore, MD, personal communication).

Ammocoete development is extremely variable. Larvae from a single cohort of spawners may persist in a stream for 5–18 yr before metamorphosing (Manion and Smith 1978). This greatly complicates research on lamprey population dynamics, and has important implications for management programs. The presence of many year classes of larvae at the same time and the lack of a good age criterion (Purvis 1979) make it difficult to study survival rates, developmental times, annual productivity, and density dependent effects in natural streams. The use of a series of natural barriers in the Big Garlic River, Michigan, was an ingenious way of getting around some of these difficulties (Manion and Smith 1978). In the context of pest management, the phenomenon introduces considerable time lags into controls aimed at the spawning adult stage (Smith et al. 1974), and complicates the determination of an economic injury level (see below).

Ammocoete growth and survival are highly dependent on temperature and population density (Manion and Smith 1978). The larvae feed on detritus and microorganisms, particularly diatoms, in the soft bottom materials in which they burrow (Applegate 1950; Manion and McLain 1971; Moore 1980). A gradual downstream movement of larvae occurs as ammocoetes leave their burrows in response to high water levels (Manion and McLain 1971), the stress of density, and external disturbances (Manion and Smith 1978) and must become reestablished on the stream bottom. Competition for food and a suitable substrate is a likely mechanism for the observed dependence of growth and survival on density. The specific, but different, habitat requirements for spawning and larval establishment place limits on the types of streams which provide the necessary conditions for complete development. This situation is exploitable, both for identifying potential production areas to be monitored, and possibly as a means of control by environmental modification.

Treatment of streams with the chemical lampricide TFM is currently the primary lamprey control measure (Applegate et al. 1961; Howell et al. 1964; Smith et al. 1974). Several of the problems outlined above for a unilateral chemical control program potentially exist in the case of using TFM as the principal lamprey control measure. It is possible that lampreys may develop resistance to TFM or to the synergist 5, 2′-dichloro-4′-nitro-salicylanilide, although the long generation time of the species will retard the process. TFM is highly toxic to mammals in its concentrated form, is stable and is not readily metabolized (Applegate et al. 1961). The nature of lampricide applications is such that essentially all of the chemical enters the general stream environment, and, in that sense, misses the intended target. TFM has produced undesired fish mortality when the "maximum allowable concentration" has been exceeded, either through error or due to variations in stream volume or water quality (Applegate et al. 1961; Smith et al. 1974). Unusually large fish kills have occurred in 3% of the stream treatments (Dahl and McDonald 1980). Certain species of fish are particularly susceptible to TFM poisoning; in general, fish are more susceptible during spawning than at other times. Fish kills have been considered to be one of the costs of lamprey control, to be minimized along with other costs (Dahl and McDonald 1980). The application of TFM to streams in concentrations used to control larval lampreys has a major impact on the invertebrate fauna immediately following treatment, although the populations essentially recover within 6 wk to a year (Torblaa 1968). Manion and Smith (1978) indicate that "some ammocoetes survive every lampricide treatment of a stream," and that the increased survival and growth resulting from a lower population density may result in nearly the same production of adult lampreys from the treated stream. The increasing cost of TFM, uncertainty of a continued supply, and the cost and difficulty of obtaining registrations for chemical pesticides are major limitations to this method of lamprey control (Smith and Tibbles 1980).

On the other hand, TFM is an effective, highly selective lampricide when properly used (Applegate et al. 1961). The long larval development period means that single applications at intervals of several years can effectively and immediately reduce the production of parasitic lampreys from that stream (Lawrie 1970). For these reasons the use of lampricides is a valuable control technique which has a place in an IPM program for the sea lamprey.

The toxicity and selectivity of TFM is greatly affected by water quality factors (Applegate et al. 1961; Smith et al. 1974). Expensive and time-consuming bioassay methods are currently used to determine the minimum lethal and maximum allowable concentrations before each application. Modeling the chemical and physiological interactions determining these concentrations may lead to simpler chemical analyses which provide the needed information. Given a model of TFM toxicity under various water quality conditions, it should also be possible to adjust the concentration of lampricide to produce a particular level of ammocoete mortality. As discussed above, complete control is not necessarily desribale — rather, the goal may be to maintain the population just below the economic injury level.

Monitoring larval development, which varies greatly from stream to stream, currently establishes the need for chemical treatments, timed to prevent the ammocoetes from reaching the metamorphic stage. A more thorough understanding of the factors determining the larval developmental period, combined with phenological models of the development process, may eventually supplement or replace this expensive biological monitoring. Treatments should be timed within the year to avoid spawning runs of desirable fish species, critical periods in the life cycle of stream invertebrates, and the relatively nonsusceptible early embryonic stages of lampreys (Piavis and Howell 1975). Modeling these ecological states as functions of environmental factors, particularly stream temperature, could help to optimize the benefit of the chemical control.

The use of chemical lampricides has been associated with changes in the sex ratio of adult lampreys in the Great Lakes (Torblaa and Westman 1980). It has been suggested that this reflects a natural population control mechanism (Smith 1971) or is itself a result of the chemical treatments (Manion and Smith 1978; Purvis 1979). Modeling of lamprey population dynamics might contribute to an understanding of the causes of this phenomena, and could certainly provide some prediction of the consequences.

The factors initiating lamprey metamorphosis are still not understood (Youson 1980). Age is apparently not a significant factor (Manion and Smith 1978). Size, growth rate, and temperature conditions may be important, but are insufficient to account for transformation (Potter 1980; Purvis 1980). Potter stated that the larval period is typically 6–8 yr, and considered the extremely long developmental periods observed in the Big Garlic River (Manion and Smith 1978) to be an anomaly. Downstream migration of newly transformed adults takes place primarily in the fall, and usually follows a drop in water temperature and rise in water level (Manion and Smith 1978). Trapping newly metamorphosed lampreys as they move downstream is a possible control measure, but this activity occurs over a 6-mo period and is greatest at high stream volumes when traps operate least efficiently (Applegate 1950).

There would be little interest in sea lamprey biology or control were it not for the activities of the parasitic phase adults. The important processes involved in this phase are dispersal, mortality, and parasite/host interactions. Very little is known about any of these processes (Smith et al. 1974). Moore et al. (1974) have shown that adult lampreys may move long distances in all directions, with interchange among the various Great Lakes. There is considerable seasonal variation in the depth at which lampreys may be captured (Applegate 1950; Farmer 1980). Natural mortality rates in the lakes have not been determined, but adult lampreys appear to have few natural enemies (Applegate 1950). The parasitic phase lasts from the fall or spring of one year to the spring 12–20 mo later (Applegate 1950). The adults grow throughout this period, most rapidly in late summer and fall and only very slowly in the winter (Farmer 1980). The great variation in size of parasitic lampreys is probably related to the length of time spent in the lake (Applegate 1950; Farmer 1980). Farmer discussed the behavior and physiology of feeding in adult lampreys. Pycha (1980) and Youngs (1980) presented methods for estimating lamprey-induced mortality of lake trout. There is a great need for further quantitative studies and modeling of the survival, movement, and attack dynamics of parasitic phase lampreys. A possible control technique relating to this phase is the breeding and release if resistant host fishes, involving either attack evasion or tolerance to injury.

Sexual maturation involves an interplay of neural and hormonal processes which is poorly understood (Larsen 1980). Behavioral and physiological events associated with maturation include the cessation of feeding, the location of stream mouths, upstream migration, and the final differentiation and development of gametes sometime before or shortly after arrival at the spawning grounds. Fecundity is related to body size (Applegate 1950), which in turn is a function of energy reserves accumulated during the parasitic phase (Larsen 1980). This would undoubtedly depend on the duration of the parasitic phase and on the energetics of predatory and migratory behavior.

It is not clear whether or not sea lampreys return to spawn in the same stream in which they developed (Larsen 1980). If this were the case, the potential would exist for interfering with the orientation of migrating lampreys. Temperature, current, and the presence of an esablished ammocoete population (Teeter 1980) provide the major external cues for the location of stream mouths. The initiation of upstream migration is favored by dark nights and water temperatures above 4.4°C, with the greatest activity occurring at 10–18°C (Applegate 1950).

Having discussed the individual components of the population dynamics of the sea lamprey (Fig. 2), some general comments may now be made concerning the prospects for developing an IPM program for this species.

A major factor hindering the development of pest management strategies for the sea lamprey will be the difficulty of establishing economic injury levels, either empirically or through modeling. The long and variable larval period introduces a considerable time lag between a major control point — the manipulation of larval survival — and subsequent damage to fish by the parasitic phase. The number of newly transformed adults migrating downstream might provide a better measure of the number of parasitic adults expected to enter a lake, but there are currently no effective control measures which can be applied at that point if the need for artificial control is indicated. A further complication is the fact that dozens of streams serve as sources of parasitic adults for each Great Lake. Economic injury to the fish occurs in a single lake, but the need for control must be determined in the individual streams. The classification of streams on the basis of potential for lamprey production may help in evaluating each stream's contribution to the total adult pool, and thus in deciding how many and which streams require treatments, and at what level of control. The dynamics of the parasitic phase are so poorly understood right now, however, that it will be difficult to establish what number of adults constitutes an economic threat. Thus the bioeconomics of lamprey control, cited by Lawrie (1970) and Smith (1971) as essential, but unknown, remain to be worked out.

Existing fish population models are for the most part inadequate for use in the study of lamprey population dynamics. For example, the immature stages are seldom considered, although the importance of early-life-stage mortality to total recruitment has been recognized by some workers in fisheries (Cushing 1975; Leggett 1977; Polgar 1977). Lett et al. (1975) and Walters (1980) developed models of adult sea lamprey interactions with lake trout stocks. The models represent good starting points and demonstrate the important role that models can play in pest management, but suffer from a lack of quantitative biological data. Much additional modeling work, supported by appropriate research, is needed.

Absolute population estimates are needed in order to work out survival rates, density dependent effects, and other population dynamics parameters, and to make use of the concept of the economic injury level. This requires quantitative sampling techniques. Estimates of parasitic-phase lamprey numbers are usually based on mark–recapture data, wounding and scarring rates, and weir catches. Ammocoete populations are typically sampled by using electroshockers or low concentrations of lampricide to stimulate the larvae to leave their burrows. There is an urgent need for further development of sampling techniques.

The high fecundity of the sea lamprey may represent an adaptation to high natural mortalities in its native habitat. The fact that the lamprey is a prolific pest in the Great Lakes suggests that it may have left its mortality sources behind as it passed through the Welland Canal. This is a familiar pattern among exotic insect pests. A comparative study of lamprey population dynamics in various parts of its range may suggest management techniques that can be applied in the Great Lakes. If the missing mortality factor is environmental, then perhaps the environment can be manipulated or restructured. If natural enemies are lacking, then the introduction or improved management of diseases, parasites, predators, or competitors may be called for. If fish populations in the Great Lakes are poorly adapted to the presence of the sea lamprey, then genetic improvement of the fish stocks may reduce the lamprey's impact. Density dependent mortalities operating during spawning and during the larval period represent starting points for a management system based on natural regulatory factors.

The fact that responsibility for carrying out lamprey control actions belongs to government agencies rather than private individuals, as is generally true in agricultural pest control, will facilitate the implementation and operation of a large-scale IPM program. However, the effort may be hindered by "the large number of semi-independent political entities" involved in the management of Great Lakes fishery resources (Paulik 1969). The coordination of management efforts over a large geographic area is difficult even without the additional "burden of political constraints."

In conclusion, the prospects for applying the principles of integrated pest management to the sea lamprey problem are good, but there are many challenges ahead in the areas of research and implementation. A prerequisite to the development of an IPM program is a thorough knowledge of the Great Lakes fish community, the biology and ecology of the sea lamprey, and possible control methods. The contributions to this symposium represent work directed to filling these needs.

APPLEGATE, V. C. 1950. Natural history of the sea lamprey, *Petromyzon marinus*, in Michigan. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. 55: 237 p.

APPLEGATE, V. C., J. H. HOWELL, J. W. MOFFETT, B. G. H. JOHNSON, AND M. A. SMITH. 1961. Use of 3-Trifluoromethyl-4-nitrophenol as a selective sea lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 1: 35 p.

ARNOLD, G. W., AND C. T. DEWIT [ed.]. 1976. Critical evaluation of systems analysis in ecosystems research and management. Centre Agric. Publ. Docu. Wageningen, The Netherlands. 108 p.

BARANOV, TH. I. 1918. On the question of the biological basis of fisheries. Nauch. Issled. Ikhtiol. Inst., Izv. 1(1): 81–128. (In Russian)

BARR, R. O., P. C. COTA, S. H. GAGE, D. L. HAYNES, A. N. KHARKAR, H. E. KOENIG, K. Y. LEE, W. G. RUESINK, AND R. L. TUMMALA. 1973. Ecologically and economically compatible pest control. Ecol. Soc. Aust. Mem. 1: 241–264.

BARTLETT, B. R. 1956. Natural predators. Can selective insecticides help to preserve biotic control? Agric. Chem. 11(2): 42–44, 107, 109.

BELL, F. W. 1978. Food from the sea: The economics and politics of ocean fisheries. Westview Press, Boulder, CO.

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. Fishery Investigations Series 2, Vol. 19. Ministry of Agric., Fisheries and Food, London.

BEYER, J. E., AND G. C. LAURENCE. 1980. A stochastic model of larval fish growth. Ecol. Model. 8: 109–132.

CLARK, C. W. 1973. The economics of overexploitation. Science 181: 630–34.

1976. Mathematical bioeconomics: the optimal management of renewable resources. John Wiley and Sons, New York, NY. 352 p.

CROFT, B. A., J. L. HOWES, AND S. M. WELCH. 1976. A computer-based, extension pest management delivery system. Environ. Entomol. 5: 20–34.

CUSHING, D. 1975. Fisheries resources of the sea and their management. Oxford Univ. Press, Oxford.

DAHL, F. H., AND R. B. MCDONALD. 1980. Effects of control of the sea lamprey (*Petromyzon marinus*) on migratory and resident fish populations. Can. J. Fish. Aquat. Sci. 37: 1886–1894.

DALE, M. B. 1970. Systems analysis and ecology. Ecology 51: 2–16.

DAVIS, R. M. 1977. Evolution of computers and computing. Science 195: 1096–1102.

DEANGELIS, D. L., D. K. COX, AND C. C. COUTANT. 1980.

Cannibalism and size dispersal in young-of-the-year largemouth bass: experiment and model. Ecol. Model. 8: 133–48.

Doutt, R. L., and R. F. Smith. 1971. The pesticide syndrome —diagnosis and suggested prophylaxis, p. 3–15. *In* C. B. Huffaker [ed.] Biological control. Plenum, New York, NY.

Entomological Society of Canada. 1974. Systems approach to pest management: proceedings of a symposium. Questiones entomologicae 10: 153–186.

EPA. 1978. Farmers and the environment. EPA Journal Reprint. U.S. Environ. Prot. Agen. April, 1978. 24 p.

Farmer, G. J. 1980. Biology and physiology of feeding in adult lampreys. Can. J. Fish. Aquat. Sci. 37: 1751–1761.

Garfinkel, D. 1962. Digital computer simulation of ecological systems. Nature 194: 856–857.

Geier, P. W., and L. R. Clark. 1960. An ecological approach to pest control. Proc. Tech. Meet. Inter. Union. Conserv. Nature Nat. Res., Warsaw. 8: 10–18.

Giese, R. L., R. M. Peart, and R. T. Huber 1975. Pest management, a pilot project exemplifies new ways of dealing with agricultural pests. Science 187: 1045–1052.

Glass, E. H. [coord.]. 1975. Integrated pest management: rationale, potential, needs and implementation. Entomol. Soc. Am. Spec. Publ. 75–2: 141 p.

Gulland, J. A. 1969. Manual of methods for fish stock assessment. Part I. Fish population analysis. FAO Man. Fish. Sci. No. 4. FAO, Rome.

1974. The management of marine fisheries. Univ. Washington Press, Seattle, WA.

1977. The analysis of data and development of models, p. 67–95. *In* J. A. Gulland [ed.]. Fish population dynamics. John Wiley and Sons, New York, NY.

Hall, C. A. S., and J. W. Day Jr. 1977. Ecosystem modeling in theory and practice. Wiley-Interscience, New York, NY. 684 p.

Hanson, L. H., and P. J. Manion. 1978. Chemosterilization of the sea lamprey (*Petromyzon marinus*). Great Lakes Fish. Comm. Tech. Rep. 29: 15 p.

1980. Sterility method of pest control and its potential role in an integrated sea lamprey (*Petromyzon marinus*) control program. Can. J. Fish. Aquat. Sci. 37: 2108–2117.

Hardin, G. 1968. The tragedy of the commons. Science 162: 1243–1248.

Haynes, D. L. 1971. Pest management and the cereal leaf beetle. A talk presented at the North Central Branch Meeting of the Entomol. Soc. Am., March 23–25. Chicago, IL.

Haynes, D. L., R. K. Brandenburg, and P. D. Fisher. 1973. Environmental monitoring network for pest management systems. Environ. Entomol. 2: 889–99.

Haynes, D. L., and R. L. Tummala. 1978. Application of computer technology to pest management, p. 181–201. *In* E. H. Smith and D. Pimentel [ed.] Pest control strategies. Academic Press, New York, NY.

Howell, J. H., E. L. King Jr., A. J. Smith, and L. H. Hanson. 1964. Synergism of 5,2′-dichloro-4′-nitro-salicylanilide and 3-trifluoromethyl-4-nitrophenol in a selective lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 8: 21 p.

Huffaker, C. B. 1978. The future of integrated pest management. EPA Journal Reprint, U.S. Environ. Prot. Agen. April, 1978. p. 7, 22–24.

Huffaker, C. B., R. F. Smith, and A. P. Gutierrez. 1976. The need for systems analysis and its use in the US/IBP integrated pest management project, p. 209–216. *In* R. L. Tummala, D. L. Haynes, and B. A. Croft [ed.] Modeling for pest management. Michigan State Univ., East Lansing, MI.

Hunn, J. B., and W. D. Youngs. 1980. Role of physical barriers in the control of sea lamprey (*Petromyzon marinus*). Can. J. Fish. Aquat. Sci. 37: 2118–2122.

Jeffers, J. N. R. 1978. An introduction to systems analysis with ecological applications. University Park Press, Baltimore, MD. 198 p.

Johnson, D. R. 1959. Management techniques now available to fisheries management agencies, their background and use, p. 9–15. *In* J. A. Crutchfield [ed.] Biological and economic aspects of fisheries management. Univ. Washington, Seattle, WA.

King, C. E., and G. J. Paulik. 1967. Dynamic models and the simulation of ecological systems. J. Theor. Biol. 16: 251–67.

Koenig, H. E. 1974. Ecology, economics and technological development: a sociocybernetic perspective. Questiones entomologicae. 10: 155–164.

Koenig, H. E., D. L. Haynes, and P. D. Fisher. 1976. Management of the environment, p. 344–382. *In* S. J. Bernstein [ed.] Computers in public administration. Pergamon Press, New York, NY.

Larkin, P. A. 1971. Simulation studies of the Adams River sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board. Can. 28: 1493–1502.

Larsen, L. O. 1980. Physiology of adult lampreys, with special regard to natural starvation, reproduction, and death after spawning. Can. J. Fish. Aquat. Sci. 37: 1762–1779.

Lawrie, A. H. 1970. The sea lamprey in the Great Lakes. Trans. Am. Fish. Soc. 99(4): 766–775.

Leggett, W. C. 1977. Density dependence, density independence, and recruitment in the American shad (*Alosa sapidissima*) population of the Connecticut River, p. 3–17. *In* W. Van Winkle [ed.]. Assessing the effects of power-plant-induced mortality on fish populations. Pergamon Press, New York, NY.

Lett, P. F., F. W. H. Beamish, and G. J. Farmer. 1975. System simulation of the predatory activities of sea lampreys (*Petromyzon marinus*) on lake trout (*Salvelinus namaycush*). J. Fish. Res. Board Can. 32: 623–631.

Luckmann, W. H., and R. L. Metcalf. 1975. The pest-management concept, p. 3–35. *In* R. L. Metcalf and W. H. Luckmann [ed.]. Introduction to insect pest management. John Wiley and Sons, New York, NY.

Manion, P. J., and L. H. Hanson. 1980. Spawning behavior and fecundity of lampreys from the upper three Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1635–1640.

Manion, P. J., and A. L. McLain. 1971. Biology of larval sea lampreys (*Petromyzon marinus*) of the 1960 year class, isolated in the Big Garlic River, Michigan, 1960–65. Great Lakes Fish. Comm. Tech. Rep. 16: 35 p.

Manion, P. J., and B. R. Smith. 1978. Biology of larval and metamorphosing sea lampreys, *Petromyzon marinus*, of the 1960 year class in the Big Garlic River, Michigan, Part II, 1966–72. Great Lakes Fish. Comm. Tech. Rep. 30: 35 p.

Metcalf, R. L., and W. H. Luckmann. [ed.] 1975. Introduction to insect pest management. John Wiley and Sons, New York, NY. 587 p.

Metcalf, R. L., and R. A. Metcalf. 1975. Attractants, repellents, and genetic control in pest management, p.

275–306. *In* R. L. Metcalf and W. H. Luckmann [ed.] Introduction to insect pest management. John Wiley and Sons, New York, NY.

Mills, J. R. 1978. IPM: Evolution or revolution? EPA Journal Reprint. U.S. Environ. Prot. Agen. April, 1978. p. 6, 21–22.

Moore, H. H., F. H. Dahl, and A. K. Lamsa. 1974. Movement and recapture of parasitic-phase sea lampreys (*Petromyzon marinus*) tagged in the St. Marys River and Lakes Huron and Michigan, 1963–67. Great Lakes Fish. Comm. Tech. Rep. 27: 19 p.

Moore, J. W. 1980. Feeding of larval lampreys. Can. J. Fish. Aquat. Sci. 37: 1658–1664.

National Academy of Sciences. 1969. Insect pest management and control. NAS, Washington, D.C. Publ. 1695: 508 p.

Park, R. A., (and 24 others). 1974. A generalized model for simulating lake ecosystems. Simulation 21: 33–50.

Patten, B. C. [ed.] 1971–76. Systems analysis and simulation in ecology. 5 volumes. Academic Press, New York, NY.

Paulik, G. J. 1969. Development of a comprehensive simulation model of the fish resources of the Great Lakes, p. 11–20. *In* Systems analysis for Great Lakes water resources. Proc. 4th Symp. Water Resour. Res., Ohio St. Univ., Water. Resour. Cent.

Piavis, G. W., and J. H. Howell. 1975. Effects of 3-trifluoromethyl-4-nitrophenol (TFM) on developmental stages of the sea lamprey. U.S. Fish Wildlife Serv. Invest. Fish. Control 64: 8 p.

Polgar, T. T. 1977. Striped bass ichthyoplankton abundance, mortality, and production estimation for the Potomac River population, p. 110–26. *In* W. Van Winkle [ed.]. Assessing the effects of power-plant-induced mortality on fish populations. Pergamon Press, New York, NY.

Potter, I. C. 1980. Ecology of larval and metamorphosing lampreys. Can. J. Fish. Aquat. Sci. 37: 1641–1657.

Purvis, H. A. 1979. Variations in growth, age at transformation, and sex ratio of sea lampreys reestablished in chemically treated tributaries of the upper Great Lakes. Great Lakes Fish. Comm. Tech. Rep. 35: 36 p.

1980. Effects of temperature on metamorphosis and the age and length at metamorphosis in sea lamprey (*Petromyzon marinus*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1827–1834.

Pycha, R. L. 1980. Changes in mortality of lake trout (*Salvelinus namaycush*) in Michigan waters of Lake Superior in relation to sea lamprey (*Petromyzon marinus*) predation, 1968–77. Can. J. Fish. Aquat. Sci. 37: 2063–2073.

Regier, H. A. 1977. Fish communities and aquatic ecosystems, 134–155. *In* J. A. Gulland [ed.] Fish population dynamics. John Wiley and Sons, New York, NY.

Ricker, W. E. 1948. Methods for estimating vital statistics of fish populations. Indiana Univ. Publ. Sci. Ser. No. 15.

1977. The historical development, p. 3–26. *In* J. A. Gulland [ed.] Fish population dynamics. John Wiley and Sons, New York, NY.

Rounsefell, G. A. 1975. Ecology, utilization, and management of marine fisheries. C. V. Mosby Co., St. Louis. 516 p.

Royce, W. F. 1972. Introduction to the fishery sciences. Academic Press, New York, NY.

Ruesink, W. G. 1975. Analysis and modeling in pest management, p. 353–376. *In* R. L. Metcalf and W. H. Luckmann [ed.] Introduction to insect pest management. John Wiley and Sons, New York, NY.

1976. Status of the systems approach to pest management. Ann. Rev. Entomol. 21: 27–44.

Shoemaker, C. 1973. Optimization of agricultural pest management I: Biological and mathematical background. Math. Biosci. 16(1/2): 143–75.

Shoemaker, C. A. 1976. Management models for integrated pest control — mathematical structure and solution, p. 32–39. *In* R. L. Tummala, D. L. Haynes and B. A. Croft [ed.] Modeling for pest management. Michigan State Univ., East Lansing, MI.

1977. Pest management models of crop ecosystems, p. 545–74. *In* C. A. S. Hall and J. W. Day Jr. [ed.] Ecosystem modeling in theory and practice. John Wiley and Sons, New York, NY.

Shugart, H. H., and R. V. O'Neill. [ed.] 1979. Systems ecology. Benchmark Papers in Ecology. V.9. Dowden, Hutchinson and Ross, Stroudsburg, PA. 368 p.

Silliman, R. P. 1967. Analog computer models of fish populations. Fishery Bull. (Washington). 66: 31–46.

1969. Analog computer simulation and catch forecasting in commercially fished populations. Trans. Am. Fish. Soc. 98: 560–69.

Smith, B. R. 1971. Sea lampreys in the Great Lakes of North America, p. 207–247. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Volume 1. Academic Press, New York, NY.

Smith, B. R., and J. J. Tibbles. 1980. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936–78. Can. J. Fish. Aquat. Sci. 37: 1780–1801.

Smith, B. R., J. J. Tibbles, and B. G. H. Johnson. 1974. Control of the sea lamprey (*Petromyzon marinus*) in Lake Superior, 1953–70. Great Lakes Fish. Comm. Tech. Rep. 26: 60 p.

Smith, E. H., and D. Pimentel. 1978. Pest control strategies. Academic Press, New York, NY.

Smith, S. H. 1968. Species succession and fishery exploitation in the Great Lakes. J. Fish. Res. Board Can. 25: 667–693.

Steele, J. H. 1977. Fisheries mathematics. Academic Press, New York, NY.

Stern, V. M., R. F. Smith. R. van den Bosch, and K. S. Hagen. 1959. The integrated control concept. Hilgardia 29(2): 81–101.

Stickney, R. R. 1979. Principles of warm water aquaculture. John Wiley and Sons, New York, NY. 375 p.

Teeter, J. 1980. Pheromone communication in sea lampreys (*Petromyzon marinus*): implications for population management. Can. J. Fish. Aquat. Sci. 37: 2123–2132.

Torblaa, R. L. 1968. Effects of lamprey larvicides on invertebrates in streams. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 572: 13 p.

Torblaa, R. L., and R. W. Westman. 1980. Ecological impacts of lampricide treatments on sea lamprey (*Petromyzon marinus*) ammocoetes and metamorphosed individuals. Can. J. Fish. Aquat. Sci. 37: 1835–1850.

Tummala, R. L., and D. L. Haynes. 1977. On-line pest management systems. Environ. Entomol. 6: 339–49.

Tummala, R. L., D. L. Haynes, and B. A. Croft. [ed.] 1976. Modeling for pest management: concepts, techniques and applications. Michigan State Univ., East Lansing, MI. 247 p.

Tummala, R. L., D. L. Haynes, and T. C. Edens. 1978. Modern pest management systems. Paper presented at 5th National Systems Conference, PAU Luchiana, India, September 4–6.

Tummala, R. L., W. G. Ruesink, and D. L. Haynes. 1975. A discrete component approach to the management of the cereal leaf beetle ecosystem. Environ. Entomol. 4. 175–86.

Usinger, R. L. 1971. Introduction to aquatic entomology: A. Principles and practices, p. 3–49. *In* R. L. Usinger [ed.] Aquatic insects of California. Univ. California Press, Berkeley, CA.

Van Winkle, W. [ed.]. 1977. Assessing the effects of power-plant-induced mortality in fish populations. Pergamon Press, New York, NY.

Varadarajan, R. V. 1979. Application of modern control theory to the management of pest ecosystems. Ph.D. thesis, Michigan State Univ., East Lansing, MI, 167 p.

Walters, C. J. 1969. A generalized computer model for fish population studies. Trans. Am. Fish. Soc. 98: 505–512.

Walters, C. J., G. Steer, and G. Spangler. 1980. Responses of lake trout (*Salvelinus namaycush*) to harvesting, stocking, and lamprey reduction. Can. J. Fish. Aquat. Sci. 37: 2133–2145.

Watt, K. E. F. 1955. The choice and solution of mathematical models for predicting and maximizing the yield of a fishery. J. Fish. Res. Board Can. 13: 613–45.

1959. Studies on population productivity II. Factors governing productivity in a population of smallmouth bass. Ecol. Monogr. 29: 367–92.

1961a. Use of a computer to evaluate alternative insecticidal programs. Science 133: 706–707.

1961b. Mathematical models for use in insect pest control. Can. Entomol. (Suppl.) 19: 62 p.

1962. Use of mathematics in population ecology. Ann. Rev. Entomol. 7: 243–60.

[ed.]. 1966. Systems analysis in ecology. Academic Press, New York, NY. 276 p.

1967. A conceptional approach to mathematical modelling and computer simulation of water quality problems, p. 57–62. *In* Systems approach to water quality in the Great Lakes. Proc. 3rd Ann. Symp. Water Resour. Res., Ohio St. Univ., Water Resour. Cent.

1968. Ecology and resource management, a quantitative approach. McGraw Hill, New York, NY. 450 p.

Welch, S. M., B. A. Croft, J. F. Brunner, and M. F. Michels. 1978. PETE: an extension phenology modeling system for management of multi-species pest complex. Environ. Entomol. 7: 487–94.

Yeh, G. T. and C. F. Yeh. 1980. Mathematical modeling of the distribution of fish eggs from spawning regions of a river. Ecol. Model. 8: 97–107.

Youngs, W. D. 1980. Estimate of lamprey-induced mortality in a lake trout (*Salvelinus namaycush*) population. Can. J. Fish. Aquat. Sci. 37: 2151–2158.

Youson, J. H. 1980. Morphology and physiology of lamprey metamorphosis. Can. J. Fish. Aquat. Sci. 37: 1687–1710.

Potential Problems in the Registration of Sea Lamprey (*Petromyzon marinus*) Control Agents[1]

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It is highly probable that increased data will be required in future applications for registration of control agents to support claims of efficacy, environmental safety, and human safety for control of the sea lamprey, *Petromyzon marinus.* Alternative techniques, such as biological or physical control methods, are also encompassed by regulatory control. Pheromones, hormones, attractants, and repellents are subject to the same stringent regulations applied to purely chemical methods. Guidelines for registering live biological control agents are under review and revision, but currently such agents are regulated under the same requirements as chemicals. The irreversible act of releasing living control organisms, such as predators, parasites, or pathogens, and their possible detrimental effects on nontarget species, will require significant proof that they will not harm the ecosystem. Biologics, such as serums, vaccines, or antigens, also require registration, but the process is less complicated and requires less time for completion. Regulation of physical control devices occurs only if the method or device is offered for sale with claims as to its efficacy.

Key words: sea lamprey, sea lamprey control, *Petromyzon marinus*, lampricides, chemical registration, chemical control, biological control, physical control

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Il est fort probable qu'à l'avenir, les demandes d'immatriculation d'agents de contrôle devront être accompagnées de beaucoup plus de données à l'appui de prétentions à l'efficacité, à la sécurité de l'environnement et à la sécurité humaine pour le contrôle de la grande lamproie marine, *Petromyzon marinus.* La réglementation englobera également d'autres techniques, telles que contrôles biologiques ou physiques. Les phéromones, hormones, et substances attractives ou répulsives sont astreintes aux mêmes règlements que les méthodes purement chimiques. On est en train d'examiner et de réviser les directives concernant les agents de contrôle biologiques vivants, mais, entre temps, ces agents sont soumis aux mêmes règlements que les substances chimiques. Avant d'autoriser la mise en liberté — un acte irrévocable — d'organismes de contrôle biologique, tels que prédateurs, parasites, ou agents pathogènes, et risquer des dommages éventuels aux espèces non visées, il faudra des preuves bien étayées que ces organismes ne nuiront pas à l'écosystème. Les substances biologiques tels sérums, vaccins ou antigènes doivent aussi être immatriculées, mais le processus est moins compliqué et requiert moins de temps. Les appareils de contrôle physique ne sont réglementés que dans les cas où méthode ou appareil fait état de son efficacité lorsque mis en vente.

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CONTROL of the sea lamprey, *Petromyzon marinus*, has been achieved through the application of a variety of methods. Barrier dams, mechanical weirs, electrical weirs, selective removal by netting, and chemical toxicants have all been used with varying degrees of success. To date, the chemical agents 3-trifluoromethyl-4-nitrophenol (TFM) and 2′,5-dichloro-4′-nitrosalicylanilide (Bayer 73) have provided the most effective means of reducing populations of the sea lamprey in the Great Lakes and their tributaries.

Current environmental awareness and legislative actions require that all lamprey control measures be properly registered or licensed by the appropriate regulatory agency. In this paper we discuss variations in existing registration guidelines as they apply to the various types of control agents and how they affect registration protocols, with particular reference to sea lamprey control.

LEGISLATIVE FRAMEWORK

Control of nuisance animals by any method in

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aquatic ecosystems of the United States falls within the regulatory domain of the U.S. Environmental Protection Agency (EPA) (Office of Federal Register 1977). In the National Environmental Policy Act (NEPA) of 1969 (as amended), EPA is charged with protecting the environment and biosphere from damage by human activity and attaining the widest range of beneficial use of the environmental without degrading it, risking health or safety, or incurring other undesirable and unintended consequences.

Regulatory control covers all applicable facets of development, distribution, and use, including the manufacturing process, bulk shipment, formulation, retail packaging, labeling, interstate shipment, applicators, application rates, use patterns, and species against which a technique may legally be applied. All producers, handlers, and applicators can thus be held legally accountable if they misuse a pest control agent. Only uses described on the label or package insert are permitted, and only at the rates or under the conditions listed. Applications of chemicals or biological controls at less than or more than the approved rate are equally illegal. Likewise, the efficacy of physical controls must not be misrepresented.

More than 99% of the currently used pest control methods involve the use of chemical agents. Most of these compounds function through their inherent toxicity to the target organisms. Control of the uses of chemical pesticides and physical controls rests with EPA under authority provided by the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA) of 1947 and the amended Federal Environmental Pesticide Control Act (FEPCA) of 1972 and its subsequent amendments.

Biological controls include living agents and products derived from live organisms. Living agents usually are designated as "biological control agents," whereas their derivatives are commonly referred to as "biologics." Depending on the technique involved, viruses may be considered in either category. Biological control agents are regulated by EPA under provisions of FIFRA and FEPCA, and biologics are governed by the U.S. Department of Agriculture (USDA) under provisions of the Virus-Serum-Toxin Act of 1913 (as amended).

Chemicals or substances used as drugs or therapeutants are controlled by the U.S. Food and Drug Administration (FDA) under authority provided by the Federal Food, Drug, and Cosmetics Act of 1938 (as amended). Inasmuch as lampricides are not affected by FDA regulations, those regulations are not discussed.

Because of the high cost of research to register chemicals, many workers have urged that alternative nonchemical methods be developed. Environmentalists have also promoted this concept because of questions over possible contamination of ecosystems and long-term safety concerns. There is no question that reasonable alternatives to chemical control agents should be sought.

The premise that the process of registration will be easier and significantly less expensive for a biological or physical control than for a chemical control is not necessarily true. Some nonchemical control techniques may, indeed, be more difficult and more expensive to register. For a time, pesticide users and industry hoped that a broad "grandfather" ruling would be made that would permit uses of traditional or historically used chemicals. This was a false hope. Likewise, those who feel that living organisms or biologically produced "natural" substances will not be required to meet EPA registration guidelines are not being realistic. Rotenone, antimycin, and pyrethrums are developed from living organisms, but all are subject to the entire regulatory process. Bacterial and viral pathogens also must meet registration requirements. Questions about possible biological contamination of an ecosystem by the introduction of exotic species have been expressed by scientists and environmentalists and must be considered.

Environmental concerns regarding the various types of control techniques follow parallel lines. Registration of a chemical for use requires data on a wide variety of factors: effectiveness on the target organism; mode of action; safety or hazard to nontarget organisms, fish, and wildlife; accumulation in tissues of plants and animals that come in contact with the compound; persistence in the environment as part of the soil, water, or biota; possible movement in organisms through the food chain; degradation rates and products; possible interactions with other compounds present in the environment; hazards to humans and domestic animals, including carcinogenicity, mutagenicity, and teratology; and many questions related to environmental chemistry (Office of Federal Register 1977).

Likewise, registration of a biological control agent, such as a bacterial pathogen, will require a highly diversified research effort. Data must be developed on its effectiveness against the target organism; mode of action; hazard to nontarget organisms; possible survival in a carrier state in unaffected organisms; routes of transfer; movement through the ecosystem; persistence in the soil or water; potential contamination of food and water; possible interaction with and transfer of genetic materials to naturally occurring bacteria; possible mutation to more virulent strains; possible cross-reactions with other related human, fish, or wildlife pathogens; and questions related to the physiology and general health of the target organism (Office of Federal Register 1977).

Artificial propagation of live biological agents and the production of biologics are regulated by EPA or USDA, as appropriate. Specific guidelines and regulations cover construction, inspection, permits, licenses, facilities, organism certification, cultures and culture methods, testing procedures, production, product preparation, dosages, potency testing, diluents and preservatives, purity and sterility, containers, expiration dates, labeling, packaging, shipment, waste disposal, sanitation, and safety (Office of Federal Register 1977, 1978). Many of the requirements for biological control agents are similar to those for chemical control agents and may be equally restrictive and expensive.

Although the language of FIFRA is sufficiently broad to provide regulation of physical pest control devices under the Act, registration of the devices, per se, is not required. Regulatory concerns in this area are related only to claims for efficacy and possible misrepresentation of the product (EPA 1976).

Because of the close parallels between environmental concerns for the various types of control methods, EPA initially did not develop separate sets of guidelines for each type, but is now in the process of doing so. Currently, the same basic set of requirements (Fig. 1) is applied to all, but waivers may be granted if individual elements are not applicable to the case in hand. Special requirements may also be added in unique circumstances of use.

As the data base for a chemical grows, occasionally information is developed that will raise serious questions as to the acceptability of the compound for use as a control agent. If the pesticide has an existing registration, EPA may file notice of its concern over the alleged hazard by listing the chemical as a candidate for its Rebuttable Presumption Against Registration (RPAR) list. Sponsors of the compound then are given an opportunity to generate additional data to rebut or disprove the alleged problem. If the question cannot be resolved, the registration may ultimately be cancelled. Other compounds may be so highly toxic that EPA may declare them "TOO HAZARDOUS TO USE" for general use and may restrict existing registered uses.

In the completion of a research protocol for the registration of a pesticide, mammalian safety tests may yield highly negative results. Should the compound prove to be carcinogenic, teratogenic, mutagenic, or otherwise constitute a serious safety hazard, it will be useless to proceed with attempts to register the agent for fishery use.

Guidelines for the registration of control agents remain in a continuous state of change. As new technologies are developed, as sensitivities for detection methods increase, and as new concerns for human safety are raised, they are rapidly incorporated into the guidelines. Because changes in the guidelines are continually published in the Federal Register, it is difficult to maintain a current list of the tests required. Annually, the guidelines and regulations are brought up to date by publication in the Code of Federal Regulations.

Chemical Controls

When the U.S. Fish and Wildlife Service was charged with development of methods for control of the sea lamprey in the Great Lakes, no one realized how effective chemical control measures would be or how difficult the procedure to register or reregister lampricides would become. The time and costs required for research and development and for the reregistration of pesticides have risen tremendously in recent years. In the 1950s, when the lampricide TFM was discovered, all required studies could be performed for $25,000 in 90 d. By 1977, $8.9 million and 4 yr were needed to meet the safety requirements (St. Aubin 1977). New requirements promulgated in 1978 will increase the cost of data generation for registration of a pesticide by 46%. The average cost is now $11.9 million (EPA 1978a).

The 1978 amendments will significantly increase the number of tests needed to register new lampricides or reregister TFM and Bayer 73 (EPA 1975, 1978b, c). Major changes in requirements were made in mutagenicity and mammalian safety tests. Eight mutagenicity tests are now required as opposed to the single test required earlier on both TFM and Bayer 73. This change will increase the cost from $1,500 to $55,000. Included in the new mammalian safety tests are a reproduction test, a second teratology test, additional metabolism tests, and some optional requirements, which may be waived for given compounds (Table 1). In environmental chemistry, new requirements involve physical-chemical degradation, metabolism studies in water and sediment (extension of work already completed), microbe-pesticide interactions, dispersion, field dissipation and accumulation (Table 1). These studies will cost an additional $300,000.

Sometimes the interaction of pesticides with environmental contaminants such as other pesticides or naturally occurring substances causes an increase in the toxicity to nontarget organisms or a decrease in the efficacy of a treatment. Such interactions may confuse and complicate the registration process. Several investigators have reported that contaminants influence the activity of management chemicals in aquatic systems. For example, detergents are known to interact with pesticides and metals to cause increased toxicity to aquatic life (Solon et al. 1969; Solon and Nair 1970; Calamari and Marchetti 1973). Heavy-metal contaminants are often present in industrial effluents, and pesticides may occur in agricultural runoff. Ferguson and Bingham (1966) and Marking and Mauck (1975) found that fish in a pesticide contaminated area may be more susceptible to toxic substances than those in uncontaminated areas because of the combined activity of the pesticides and the other toxic substances. Fish containing residues of PCBs may be unable to detoxify other contaminants they receive from the environment (Bills and Marking 1977).

Additional environmental contaminants, such as nitrite or ammonia at high levels, may greatly affect the activity of lampricides. In tests at the La Crosse

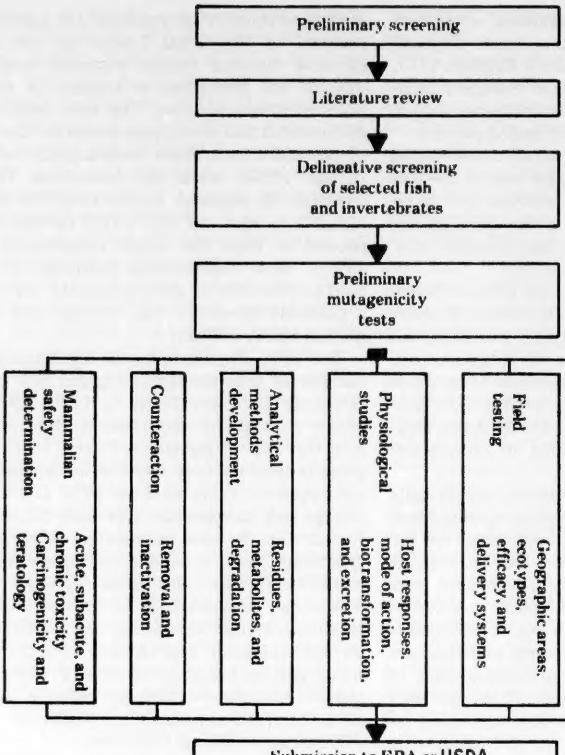
Preliminary screening
Literature review
Delineative screening of selected fish and invertebrates
Preliminary mutagenicity tests
Toxicity to target and nontarget organisms
Fish, invertebrates, birds, and plants
Field testing
Geographic areas, ecotypes, efficacy, and delivery systems
Physiological studies
Host responses, mode of action, biotransformation, and excretion
Analytical methods development
Residues, metabolites, and degradation
Counteraction
Removal and inactivation
Mammalian safety determination
Acute, subacute, and chronic toxicity Carcinogenicity and teratology
Submission to EPA or USDA for registration
Agency review and comment
Response to EPA or USDA comments – required further studies
Agency review and comment
Response to EPA or USDA comments
REGISTRATION or final action
Reregistration in 5 years

FIG. 1. Flow chart of activities required for the registration of fish control agents by the Environmental Protection Agency (EPA) or by the Department of Agriculture (USDA).

TABLE 1. Studies to support submissions for the registration or reregistration of pesticides used in aquatic environments.[a]

Part 1 — Chemistry requirements

- A. Environmental chemistry
  - 1. Physical–chemical degradation
    - a. Hydrolysis
    - b. Photodegradation
  - 2. Metabolism
    - a. Anaerobic aquatic metabolism
    - b. Aerobic aquatic metabolism
    - c. Effects of microbes on pesticides
    - d. Effects of pesticides on microbes
  - 3. Mobility
    - a. Adsorption
    - b. Water dispersal
  - 4. Field dissipation
    - a. Soil (food use)
    - b. Water
  - 5. Accumulation
    - a. Rotational crop (food use)
    - b. Irrigated crop
    - c. Fish accumulation — laboratory
    - d. Fish accumulation — field (aquatic nonfood use)
- B. Special chemistry requirements
  - 1. Tolerance clearance

Part 2 — Hazard evaluation: wildlife and aquatic organisms

- A. Avian and mammalian testing
  - 1. Avian single-dose oral LD50 — mallard or bobwhite
  - 2. Avian dietary LC50 — mallard and bobwhite
  - 3. Mammalian acute toxicity — representative species
  - 4. Avian reproduction — mallard and bobwhite
  - 5. Simulated and actual field testing for mammals and birds
- B. Aquatic organism testing
  - 1. Fish acute LC50 — rainbow trout and bluegill
  - 2. Acute toxicity to aquatic invertebrates — daphnids, amphipods, stone flies, or mayflies
  - 3. Acute toxicity to estuarine and marine organisms — shrimp (96-h LC50); crab (96-h LC50); estuarine or marine fish (96-h LC50); American oyster (48-h LC50 or 96-h EC50)
  - 4. Embryolarvae and life-cycle studies of fish and aquatic invertebrates — fathead minnow
  - 5. Aquatic organism toxicity and residue studies — channel catfish or carp; brook trout, rainbow trout, bass, bluegill, northern pike, or walleye; oysters or freshwater clams; *Daphnia* spp., *Gammarus* spp., crayfish, or mayfly nymphs
  - 6. Simulated or actual field testing for aquatic organisms

Part 3 — Hazard evaluation: humans and domestic animals

- A. Acute testing
  - 1. Acute oral toxicity study — rat
  - 2. Acute dermal toxicity study — albino rabbit
  - 3. Acute inhalation toxicity study — rat
  - 4. Primary eye irritation study — albino rabbit
  - 5. Primary dermal irritation study — albino rabbit
  - 6. Dermal sensitization study — albino guinea pig
  - 7. Acute delayed neurotoxicity study — chicken (hen)
- B. Subchronic testing
  - 1. Subchronic oral dosing studies — rat (90 d), dog (6 mo)
  - 2. Subchronic 21-d dermal toxicity study — albino rabbit
  - 3. Subchronic 90-d dermal toxicity study — albino rabbit
  - 4. Subchronic inhalation toxicity study — rat
  - 5. Subchronic neurotoxicity study — chicken (hen)
- C. Chronic testing
  - 1. Chronic feeding study — rat
  - 2. Oncogenicity studies — rat and mouse
  - 3. Teratogenicity studies — (two species) rat, mouse, hamster, or rabbit
  - 4. Reproduction study — rat

TABLE 1 (*Concluded*)

D. Mutagenicity testing
  1. Gene mutation detection tests — three of the following
    a. Bacteria
    b. Eukaryotic microorganisms
    c. Insects
    d. Mammalian somatic cells in culture
    e. Mouse specific locus test
  2. Chromosomal aberration detection tests — three of the following
    a. In vivo cytogenetic tests in mammals
    b. Insect tests for heritable chromosomal effects
    c. Dominant lethal effects in rodents
    d. Heritable translocation tests in rodents
  3. Primary DNA damage detection tests — two of the following
    a. DNA repair in bacteria
    b. Unscheduled DNA repair synthesis in mammalian cells
    c. Mitotic recombination or gene conversion in yeast
    d. Sister-chromatid exchange in mammalian cells

E. Special testing
  1. General metabolism studies — rat

F. Special requirements
  1. Domestic animal safety testing

[a] Excerpted from EPA (1978b, c).

National Fishery Research Laboratory, the toxicity of combinations of TFM and nitrite was greater than that of each individual compound, indicating that nitrite may be a factor in fish kills (Meyer 1978).

Regulatory agencies are concerned that pesticide use under certain conditions may cause formation of carcinogenic nitrosamines. Naturally occurring nitrite may react with amines derived from pesticides to form nitrosamines. Nitrosating agents are available not only from the nitrogen cycle in aquatic environments, but also from nitrogenous compounds that occur in sewage, agricultural runoff, packing house wastes, and industrial chemicals (Environmental Research Center 1977). Regulatory agencies now require nitrosamine evaluations of all chemicals that, because of their structures, could become involved in the formation of nitrosamines. Mutagenicity and oncogenicity testing is required for all suspect compounds.

Another problematical situation involved responses by aquatic organisms to environmental variables and exposures to sublethal levels of chemicals. Cairns et al. (1976) found that exposure to sublethal levels of TFM followed by thermal shock was lethal to brown trout, *Salmo trutta*.

In light of the problems associated with contaminants, unusual water chemistries, and vulnerable physiological conditions of fishes or invertebrates, lampricides may sometimes have to be neutralized to protect populations of nontarget organisms present in the treatment area. Inadvertent fish kills are likely to receive much closer scrutiny in the future than in the past, from EPA, State environmental agencies, and environmentalists. Concern has already been expressed by municipalities and industries that use treated streams as water sources, either for drinking or for use in manufacturing process. State health departments have indicated concern about possible contamination of agricultural crops and potable water. Activated carbon effectively removes TFM from water, and other filter media might also be feasible (Dawson et al. 1976; Whitehouse 1967). Chemical agents such as potassium permanganate, chlorine, and sodium thiosulfate have been used to detoxify fish toxicants applied in large rivers (Johnson and Pasch 1975; Hocutt et al. 1973; Dawson 1975; Loeb and Engstrom-Heg 1970). Detoxification procedures for lampricides should be considered.

Another potential problem in registration is the possibility that the target organism may become resistant to a chemical agent. By 1975, 305 species of invertebrate pests had become resistant to one or more pesticides. Although plants apparently do not readily develop resistance, insects and rodents frequently do (Council on Environmental Quality 1978). It is possible that the sea lamprey may become resistant to lampricides currently used. Experience has also shown that organisms can develop resistance not only to a class of chemicals, but also to different chemical groups (Council on Environmental Quality 1978).

Another problem confronting persons trying to register lampricides relates to the development of formulations and delivery systems that will be efficacious in the many different environmental situations found in an ecosystem. The success of the lamprey control program is affected by many factors, which include the presence of lentic habitats, deltas where streams enter lakes, drop-offs, shipping channels, and offshore sand flats; the great variations in stream flow; and the inaccessibility of remote areas. Currently registered lampricide formulations work well in small to medium-sized streams, but may not be suitable for large rivers or delta areas.

A granular form of Bayer 73 is registered for sampling sea lamprey populations, but not for their eradication. Extension of the label to include Bayer 73 as a control agent will require that data be provided on efficacy and environmental concerns.

Changes in the formulations of currently registered lampricides could be accomplished without great difficulty. Additional studies that would have to be performed include acute toxicity tests to fish and invertebrates, field trials of efficacy, and residue analyses in water and fish. If a new product is intended to be a bottom formulation additional metabolism studies with microbes may be required. If a different carrier or synergist is used, the substance must meet requirements for aquatic application.

Persistence of chemicals in the environment is another problem of concern to regulatory agencies. EPA requires many studies to answer questions pertaining to environmental chemistry (Table 1). Evidence may be demanded by environmentalists that low concentrations do not produce long-term, chronic toxicities to nontarget organisms. Such questions were raised concerning TFM, but were satisfactorily answered by data developed during research on that compound.

Subtle changes in an ecosystem may occur as a result of chemical treatment. If a target species is completely or partly eliminated from an ecosystem, changes may occur in predator–prey relationships or between competing species. Behavioral changes among the various species may also result. McCraren et al. (1969) found that the bluegill, *Lepomis macrochirus*, consumed less food after an application of diuron, not because of direct effects of the chemical, but because oxygen levels were reduced. Changes in the physical and chemical characteristics of the aquatic environment as a result of a chemical treatment must also be considered, and studies to evaluate such changes may be required in the future.

Biological Controls

Biological controls include such living entities as predators, parasites, bacteria, viruses, fungi, or protozoans; naturally occurring biochemicals produced by organisms, such as hormones and pheromones; and biologics — substances produced in response to the presence of organisms or their protein. As of January 1, 1979, biological controls constituted less than 1% of the total pesticides registered in the United States, and all were used against insects. Two bacterial pathogens, three viruses, and two pheromones had been registered for use as insecticides. Another nine were being tested under Experimental Use Permits (EUP) or in field studies. Although many groups involved in pest control have expressed an interest in biological agents, only insect control has thus far provided enough market potential to stimulate serious research on a commercial scale.

Living biological control agents may be highly effective — in either positive or negative ways. Extreme caution and careful testing are required to prevent adverse environmental effects. Once an organism is released into an ecosystem as a biological control, it seldom can be retracted or eradicated. Its impact on nontarget species cannot be controlled if the agent expands its activity beyond the original target organism. Should this occur, the agent becomes a bona fide biological contaminant.

To provide effective biological control, an agent must either be (1) self-perpetuating, i.e. become established in the ecosystem, or (2) amenable to artificial culture or synthesis. Establishment requires that the agent be able to maintain itself throughout all seasons of the year, during low population cycles of the target organism, and during changes in the environment. Establishment often requires the availability of suitable alternate host organisms or prey to ensure the continued presence of the agent as the target population declines. Self-perpetuation assists in the distribution or movement of the agent throughout the ecosystem and helps provide effective coverage of the host's range (Huffaker 1971; Kilgore and Doutt 1967; Howard 1967).

The use of the ladybug beetle, *Rodolia cardinalis*, to control the cottonycushion scale, *Icerya purchasi*, on citrus is a classic example of the successful establishment of a biological agent (Lawless et al. 1977). Another highly successful program involving the control of the screwworm fly, *Callitroga americana*, is based on the availability of millions of sterile males produced under artificial culture. Without artificial culture, the technique would be impossible.

Bacillus thuringiensis and *B. popilliae* are bacterial pathogens of insects that have been registered by EPA as control agents for insects. Other bacteria, several viruses, fungi, protozoans, and nematodes have also yielded successful insect control. Again, artificial propagation of the agent is the keystone to successful implementation of the technique (Tanada 1967).

On the other hand, the inadvertent introduction of *Aphanomyces*, a pathogenic fungus, to European waters resulted in catastrophic losses among local crayfish populations. The fungus has become so well established that native crayfish are now virtually nonexistent in infected streams. Spores of the fungus are viable for extended periods, and other semi-resistant crustaceans serve as reservoirs to help maintain the pathogen. Although this example provides an illustration of negative effects of the establishment of a biological control agent, it also indicates the degree of effectiveness that can be achieved and demonstrates the basis for concerns expressed by managers, regulatory agencies, and environmentalists.

Live biological control agents for the sea lamprey remain a theoretical concept at this time. Studies on lampreys by McLain (1951) and Wilson (1967) revealed the presence of a number of helminth parasites. However, none of these organisms appear to fulfill the criteria for an effective control. The listed species lack adequate host specificity and also are debilitating, at best, rather than lethal.

Specific bacterial or viral pathogens of the sea lamprey also are unknown at this time. The likelihood of finding a suitable, highly specific bacterium is remote. Most bacterial pathogens of fish infect a variety of species and would pose a potential problem to nontarget fishes. Bacterial fish diseases are believed to be stress mediated and to be the end result of interactions of the etiological agent, the fish, and the environment (Wedemeyer et al. 1976).

Development of a biological agent that would meet regulatory requirements will require significant investments of research time and monies. This cost would probably exceed that of a chemical screening program, several times over. However, if a suitable agent could be found, the requirements for registration would be easier to fulfill, and the cost would be much less than that for a chemical control agent.

Pheromones and Hormones

The use of pheromones and hormones as control agents is an intriguing concept that has aroused considerable interest among researchers. (See also Teeter 1980). From a regulatory standpoint, pheromones represent highly specialized chemical control agents. As such, they would be subject to many of the requirements and tests required for chemicals before they could be registered for use as control agents.

Pheromones are related to two basic biological phenomena, sex and behavior. Although it is often assumed that particular pheromones — especially those related to sex — are unique to a given species, this assumption has proved to be untrue. The literature contains many instances in which the specific scent of one insect has attracted other species (Shorey and Gaston 1967). This lack of specificity can pose significant problems in the registration process.

Research on the use of hormones as pest control agents has also centered on insects. Hormones of vertebrates differ significantly from those of insects in their function and action. In fishes, pituitary glands and gonadotropins have been used successfully to induce sexual maturation or ovulation, or both. Such uses have application only in cultural situations and are not feasible in an ecosystem approach.

Knowledge of the hormones of sea lamprey is too limited to enable us to evaluate them as potential tools for lamprey control. None of the work on hormones of fish has indicated that they might have potential as biological control agents. If hormones were found to be useful for lamprey control, the biochemicals involved would be treated as chemical controls in the registration process and be subject to all tests and data requirements for such agents.

Biologics

Biologics are defined as biological products such as viruses, serums, toxins, and analogous products of natural or synthetic origin and as the antigenic or immunizing components of microorganisms intended for the diagnosis, treatment, or prevention of diseases of animals.

The technique of immunologically sterilizing adult sea lampreys by injecting serum from rabbits which have developed antibodies to gonadal tissue from lampreys is not exempt from registration. Because a serum is used to produce an antigen-antibody reaction, the technique falls within regulations of the Virus-Serum-Toxin Act. Although the technique does not relate to disease control, precedent for regulation under this Act exists in similar products used to control oestrus and conception in dogs.

Immunological sterilization could also be subject to regulation under FIFRA. In Section 162.3 of the amended Act (EPA 1975), the definition of fish poisons and repellents includes "Sex influence agents intended to control sexual development of fish. . . ."

Present regulatory policies give precedence to application of the Virus–Serum–Toxin Act within jurisdiction of USDA. Thus, the data to be collected and the legal requirements to be fulfilled are considerably fewer than those under FIFRA. A licensed facility is required to produce the needed serum and conduct appropriate tests that will ensure potency, purity, and stability, so that the product can be labeled, packaged, and shipped interstate. If efficacy of the immunological sterilization technique can be adequately demonstrated, fulfillment of registration requirements should be possible in less than 2 yr and at a cost which may be only one-tenth that of a chemical control agent.

Physical Controls

From a regulatory standpoint, the use of physical pest control methods or devices poses the least problem of all control techniques. Pest control devices are regulated under provisions of FIFRA, but registration and labeling are not required. If a device is offered for sale as a pest control device with claims for its efficacy, the manufacturer or seller must have an EPA establishment number indicating that his participation in pest control work has been approved. The Enforcement Division of EPA is responsible for determining that a device is effective for the purposes claimed, and that advertisements contain no misrepresentation in the offer for sale. No restrictions exist concerning interstate shipment of pest control devices.

Environmental concerns related to devices are not addressed under the current regulations of FIFRA and

FEPCA, except that users may be required to file Environmental Impact Statements (EIS) under NEPA 1970 (as amended), if the devices are likely to affect a substantial portion of an ecosystem.

The construction of dams, barriers, or other stream alterations is not covered under pesticide regulations. If such structures are used to control sea lampreys, registration poses few, if any, problems; rather, requirements for use permits may present significant obstacles. Both Federal and State laws must be considered, because statutes vary from state to state.

Agencies involved in the permit process include the U.S. Corps of Engineers, EPA, the Department of the Interior, and the various states affected by applications. Regulatory authority is provided under the River and Harbor Act of 1899 (as amended); the Clean Water Act of 1977 (as amended); NEPA of 1970 (as amended); the Endangered Species Act of 1973 (as amended); and Presidential Executive Orders on the preservation of wetlands and on the use of flood plains (U.S. President. Executive Order 1977a, b). In addition, the review process for Environmental Impact Statements requires involvement of the Department of the Interior in all considerations of potential effects on ecosystems. Should the device or its operation pose a safety or health hazard, the Department of Labor may also become involved under provisions of the Occupational Safety and Health Act of 1970, as amended (Library of Congress 1977).

Integrated Controls

Integrated pest control is a management concept that involves the systematic application of multiple techniques in a way that will exert maximum impact on a target organism. To the greatest degree possible, all available information on the biology of the pest species is used against itself, including such diverse elements as susceptibility to parasites or pathogens, susceptibility to toxicants, vulnerability of various life stages to habitat changes, potential usefulness of attractants and repellents, susceptibility to trapping, and the possibility of using sterilization techniques to reduce or eliminate reproduction. This information is then used to combine the various control techniques in a program that will affect as many life stages of the target species as possible, will attack the organism at the most vulnerable stage in its life history, or will reduce the amount of chemical required without a decrease in efficacy.

Integrated pest control programs involve chemical, biological, and physical control techniques, each of which is subject to its own registration or regulatory requirements. The combined use of the several control techniques does not alter these requirements, and each must still meet the required standards. On the other hand, if each of the individual techniques is approved by the regulatory agencies, registration of an integrated pest control program is not required.

Development of an integrated control program to combat the sea lamprey is already under consideration. Registration requirements pose no problems to the implementation of any program that may be developed unless the use pattern of one of the lampricides is significantly changed. If a change occurred, the registration for use of the chemical would have to be amended. However, data requirements to amend a label can generally be met by completion of basic studies to demonstrate efficacy, impacts on nontarget organisms, and residue dynamics. The costs of such studies are usually not great.

Bills, T. D., and L. L. Marking. 1977. Effects of residues of the polychlorinated biphenyl Aroclor 1254 on the sensitivity of rainbow trout to selected environmental contaminants. Progr. Fish-Cult. 39: 150.

Cairns, J. Jr., W. F. Calhoun, M. J. McGinness, and W. Straka. 1976. Aquatic organisms response to severe stress following acutely sublethal toxicant exposure. Water Resour. Bull. 12: 1233–1243.

Calamari, D., and R. Marchetti. 1973. The toxicity of mixtures of metals and surfactants to rainbow trout (*Salmo gairdneri* Rich.). Water Res. 7: 1453–1464.

Council on Environmental Quality. 1978. Environmental quality: The Ninth Annual Report of the Council on Environmental Quality. U.S. Government Printing Office, Washington, D.C. 599 p.

Dawson, V. K. 1975. Counteracting chemicals used in fishery operations: Current technology and research, p. 32–40. *In* P. H. Eschmeyer [ed.] Rehabilitation of fish populations with toxicants: A symposium. North Central Division, Am. Fish. Soc. Spec. Publ. 4.

Dawson, V. K., L. L. Marking, and T. D. Bills. 1976. Removal of toxic chemicals from water with activated carbon. Trans. Am. Fish. Soc. 105: 119–123.

Environmental Research Center. 1977. Scientific and technical assessment report on nitrosamines. U.S. Environmental Protection Agency, EPA-600/6-77-001: 107 p.

Ferguson, D. E., and C. R. Bingham. 1966. The effect of combinations of insecticides on susceptible and resistant mosquito fish. Bull. Environ. Contam. Toxicol. 1: 97–103.

Hocutt, C. H., P. S. Hambrick, and M. T. Masnik. 1973. Rotenone methods in a large river system. Arch. Hydrobiol. 72: 245–252.

Howard, W. E. 1967. Biocontrol and chemosterilants, p. 343–386. *In* W. W. Kilgore and R. L. Doutt [ed.] Pest control: Biological, physical, and selected chemical methods. Academic Press, New York, NY.

Huffaker, C. B. [ed.]. 1971. Biological control. Plenum Press, New York, NY. 511 p.

Johnson, T. L., and R. W. Pasch. 1975. Improved rotenone sampling equipment for streams. Georgia Department of Natural Resources, Federal Aid in Fish Restoration, Project F-28-R-L: 22 p.

Kilgore, W. W., and R. L. Doutt [ed.]. 1967. Pest control: Biological, physical, and selected chemical methods. Academic Press, New York, NY. 477 p.

Lawless, E. M., R. von Rumker, G. L. Kelso, K. A. Lawrence, J. D. Maloney, and E. R. Thompson. 1977. A technology assessment of biological substitutes for chemical pesticides. Midwest Res. Inst. MRI Project 3879-L: 407 p.

Library of Congress. 1977. A compilation of federal laws relating to conservation and development of our nation's fish and wildlife resources, environmental quality, and oceanography. U.S. Government Printing Office, Committee Print, Serial No. 95-B, Washington, D.C. 933 p.

Loeb, H. A., and R. Engstrom-Heg. 1970. Poisoning of the Ten Mile River. New York Fish News 32: 4–7.

Marking, L. L., and W. L. Mauck. 1975. Toxicity of paired mixtures of candidate forest insecticides to rainbow trout. Bull. Environ. Contam. Toxicol. 13: 518–523.

McCraren, J. P., O. B. Cope, and L. Eller. 1969. Some chronic effects of diuron on bluegills. Weed Sci. 17: 497–504.

McLain, A. L. 1951. Diseases and parasites of the sea lamprey, *Petromyzon marinus*, in the Lake Huron basin. Trans. Am. Fish. Soc. 81: 94–100.

Meyer, F. P. 1978. Quarterly report of progress April-June 1978; Fish Control Laboratory, La Crosse, Wisconsin and Southeastern Fish Control Laboratory, Warm Springs, Georgia. U.S. Fish and Wildlife Service, Fish Control Laboratory, La Crosse, WI. 25 p.

Office of the Federal Register. 1977. Code of Federal regulations. Title 40 — Protection of the environment. Parts 100–399. U.S. Government Printing Office, Washington, D.C. 601 p.

1978. Code of Federal regulations. Title 9 — Animals and animal products. Chapter I. Animal and plant health inspection service. Parts 0–199. U.S. Government Printing Office, Washington, D.C.

Shorey, H. H., and L. K. Gaston. 1967. Pheromones, p. 241–265. *In* W. W. Kilgore and R. L. Doutt [ed.] Pest control: Biological, physical, and selected chemical methods. Academic Press, New York, NY. 477 p.

Solon, J. M., J. L. Lincer, and J. H. Nair, III. 1969. The effect of sublethal concentrations of LAS on the acute toxicity of various insecticides to the fathead minnow (*Pimephales promelas* Rafinesque). Water Res. 3: 767–775.

Solon, J. M., and J. H. Nair, III. 1970. The effect of a sublethal concentration of LAS on the acute toxicity of various phosphate pesticides to the fathead minnow (*Pimephales promelas* Rafinesque). Bull. Environ. Contam. Toxicol. 5: 408–413.

St. Aubin, F. 1977. How much do regulations inhibit pesticide development? Pest Control 45: 16–21.

Tanada, Y. 1967. Microbial pesticides, p. 31–88. *In* W. W. Kilgore and R. L. Doutt [ed.] Pest control: Biological, physical, and selected chemical methods. Academic Press, New York, NY.

Teeter, J. 1980. Pheromone communication in sea lampreys (*Petromyzon marinus*): implications for population management. Can. J. Fish. Aquat. Sci. 37: 2123–2132.

U.S. Environmental Protection Agency. 1975. Pesticide program: Guidelines for registering pesticides in the United States. Federal Register 40(123): 26801–26928.

1976. Pest control devices and device producers; consolidation and clarification of requirements. Federal Register 41(225): 51065–51067.

1978a. Registration of pesticides in the United States: Proposed guidelines; economic impact analysis. Federal Register 43(173): 39643–39697.

1978b. Registration of pesticides in the United States: Proposed guidelines. Federal Register 43(132): 29695–29741.

1978c. Pesticide programs: Proposed guidelines for registering pesticides in the U.S.; hazard evaluation: Human and domestic animals. Federal Register 43(163): 37335–37403.

U.S. President. Executive Order. 1977a. Floodplain management, E. O. 11988. Federal Register 42(101): 26951–26957.

1977b. Protection of wetlands, E.O. 11990. Federal Register 42(101): 26961–26965.

Wedemeyer, G. A., F. P. Meyer, and L. Smith. 1976. Diseases of fishes. Book 5: Environmental stress and fish diseases. T. F. H. Publications, Inc., Neptune, NJ. 192 p.

Whitehouse, J. D. 1967. A study of the removal of pesticides from water. University of Kentucky, Water Resour. Inst. Res. Rep. 8: 175 p.

Wilson, K. A. 1967. Parasite fauna of the sea lamprey (*Petromyzon marinus* von Linné) in the Great Lakes region. M.S. thesis, Univ. Guelph, Guelph, Ont.

Development of Sea Lamprey (*Petromyzon marinus*) Larvicides[1,2]

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Larvicides are used to control sea lamprey (*Petromyzon marinus*) in the Great Lakes. These larvicides are useful because they are more toxic to sea lamprey than fish species found in the same habitat. The lampricides come from two classes of chemical compounds: (1) halonitrophenols, and (2) halonitrosalicylanilides. Selectivity of the larvicides appears to be based on the differences in the ability of sea lamprey larvae and fishes to detoxify and/or excrete the chemicals. Glucuronide conjugation is an important mechanism for detoxification of these larvicides by fish, and selectivity of larvicides may be due to differences in glucuronyl transferase activity between lamprey and fishes. If more detailed information were available on uptake, metabolism, excretion, and the biochemistry and physiology of lamprey as compared to fishes, it might be possible to design chemicals that would be more selective than those now in use.

Key words: sea lamprey, larvicides, selective toxicity, uptake, metabolism, excretion, halonitrophenols

HOWELL, J. H., J. J. LECH, AND J. L. ALLEN. 1980. Development of sea lamprey (*Petromyzon marinus*) larvicides. Can. J. Fish. Aquat. Sci. 37: 2103–2107.

On utilise des larvicides dans le contrôle de la grande lamproie marine (*Petromyzon marinus*) dans les Grands Lacs. Ces larvicides sont utiles parce qu'ils affectent la lamproie plus que les autres espèces de poissons se trouvant dans le même habitat. Les lampricides appartiennent à deux classes de composés chimiques : (1) halonitrophénols et (2) halonitrosalicylanilides. La sélectivité des larvicides semble fondée sur des différences d'aptitudes des larves de grande lamproie marine et des poissons à se désintoxiquer et/ou à excréter les substances chimiques. Un important mécanisme de désintoxication chez les poissons est la conjugaison glucuronide, et la sélectivité des larvicides peut être due à des différences d'activité de la glucuronide transférase entre la lamproie et les poissons. Si l'on connaissait mieux l'assimilation, le métabolisme, l'excrétion et la biochimie et physiologie de la lamproie comparés à ceux des poissons, il serait peut-être possible de trouver des substances chimiques plus sélectives que celles présentement en usage.

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SELECTIVELY toxic chemicals are used to control sea lamprey (*Petromyzon marinus*) in the Great Lakes. These chemicals are applied in various ways to areas inhabited by the larval stage of this lamprey. The discovery and development of chemicals to control sea lamprey has been an ongoing process since 1953. Close to 10 000 predominantly organic compounds have been tested.

This long-term screening effort has resulted in the discovery of two classes of compounds which contain chemicals that are selectively toxic to larval lamprey: (1) 15 halogenated mononitrophenols; one of these compounds, 3-trifluormethyl-4-nitrophenol (TFM), is the major toxicant used in sea lamprey control; and (2) substituted nitrosalicylanilides: 56 chemicals exhibit some selectivity for larval lamprey of which 5,2′-dichloro-4′-nitrosalicylanilide (Bayer 73) is used in lamprey control as an additive to increase toxicity of

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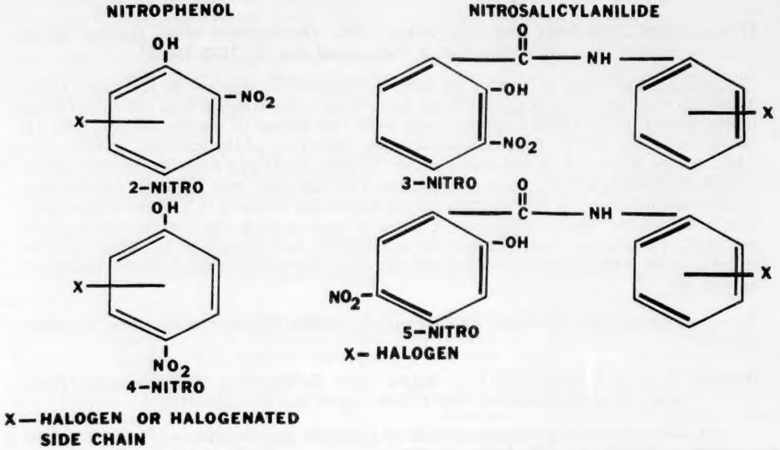
TFM and in granular formulations as a bottom releasing toxicant.

STRUCTURE ACTIVITY

The original chemical screening program set up to find selective toxic compounds for controlling sea lamprey tested a randomly selected series of predominantly organic materials (Applegate et al. 1957). With the discovery of first halogenated nitrophenols and then halogenated nitrosalicylanilides, programs were developed to test intensively related compounds within these groups. These testing programs were primarily for determining the most useful compound within the group and also relationship between their chemical structure and selective toxicity to sea lamprey (Applegate et al. 1966; Starkey and Howell (1966).

The basic structures of nitrophenols and salicylanilides which are selectively toxic to lamprey are:



In both classes of compounds the location of the nitro group is the controlling factor. Although some exceptions occur, a single halogen (or halogenated side chain, such as trifluormethyl) produces the most favorable activity: toxicity plus selectivity.

WATER–CHEMICAL INTERACTION

The effect of water chemistry on the toxicity of sea lamprey larvicides has long been recognized (Applegate et al. 1961; Howell et al. 1964). The characteristics of water which have the most noticeable effect on the toxic concentration of the lampricides are pH, total hardness, and alkalinity. The physical properties that influence the movement of chemicals across biological membranes are well defined. Generally, any molecule that is distinctly charged or is otherwise fat-insoluble, and has a molecular weight in excess of 100, is almost certainly excluded from crossing biological membranes unless a specific membrane transport mechanism exists for that particular chemical (LeFevre 1972). The effective concentrations of the lamprey larvicides 3-trifluormethyl-4-nitrophenol (TFM) and TFM synergized with 5,2′-dichloro-4′-nitrosalicylanilide (Bayer 73) were reported to be significantly increased by increased pH (Applegate et al. 1961; Howell et al. 1964; Marking and Hogan 1967; Marking and Olson 1975; Bills and Marking 1976; Dawson et al. 1975, 1977).

Applegate et al. (1961) reported the pK_a of TFM to be 6.07. The concentration of the lipid-soluble free phenol form of TFM will decrease, and that of the phenolate ion form will increase rapidly with increases in pH above 6.07. Hunn and Allen (1974) showed a much slower uptake of TFM by rainbow trout (*Salmo gairdneri*) at higher pH values. They also reported that muscle residues of TFM in channel catfish (*Ictalurus punctatus*) exposed to 1 mg/L of the lampricide for 12 h at pH 6 were 3.21 μg/g, whereas those of fish exposed to the lampricide at pH 9 contained 0.03 μg/g of TFM in muscle. As the pH increases, the concentration of available free phenol decreases, and thus the concentration of the toxic form of the lampricide available to both larval lamprey and nontarget organisms decreases. Also, Dawson et al. (1975) noted that the toxicity of TFM to larval sea lamprey was significantly lower in hard water than in soft water, especially at higher pH values. The possibility of a complex ion forming between the ionized form of TFM and divalent cations (Ca^{+2}) in the harder water could account for the effect by shifting the ionization equilibrium, and resulting in a decrease in the concentration of available free phenol. The phenolate ion and complex ions of TFM apparently do not cross the gill membrane. Thus, the toxicity of the lampricide is decreased when the concentration of the lipid-soluble free phenol is decreased by these equilibrium reactions. Meredith (1971) reported a loss in molluscicidal activity of Bayer 73 at pH values below 7, due to precipitation. However, the lower toxicity of Bayer 73 at pH values below 7 was not found in studies on lamprey (Dawson et al. 1977) and 13 species of fish (Bills and Marking 1976). The solubility of Bayer 73, even at the lower pH values, is probably well above the concentrations of this chemical that are toxic to these animals. This low degree of solubility at pH values below 7 can cause problems with dispersing the chemical into natural waters to obtain lampricidal concentrations.

The toxicity of the lampricides is dependent on the form of the chemical present and the solubility of the chemical in water. The effect of pH and hardness on the toxicity of the lampricides is an example of the effects that physical factors may exert on the chemistry of compounds in the aquatic environment and their subsequent effects on biological organisms.

PHARMACOLOGY

The mode of action of the lampricides remains undefined; however, Kawatski and McDonald (1974) reviewed the literature and conducted research which supported the hypothesis that low levels of TFM uncouple oxidative phosphorylation and that high concentrations inhibit oxygen utilization. Hunn (1971) established that white suckers (*Catostomus commersoni*) exposed to an acutely lethal concentration of TFM died of a lactic acidosis. The increase in lactic acid and glucose in plasma of white suckers exposed to TFM indicates blockage of glucose utilization and fits the physiological pattern expected from inhibition of metabolic enzymes of the terminal respiratory pathway.

The dynamics of the lampricides in fish is dependent on biotransformation, filling of tissue pools, and excretion, as well as uptake of the chemicals. Lech and Costrini (1972) identified the major metabolite of TFM in bile of fish exposed to the lampricide as the glucuronide conjugate. Subsequent studies (Lech 1973; Lech et al. 1973; Hunn and Allen 1975a, b; Schultz et al. 1979) showed that glucuronide conjugation and biliary excretion of TFM is an important mechanism for detoxification of TFM by fish. Lech and Statham (1975) showed that the differences in glucuronyl transferase activity between lamprey and higher fishes may account for a large part of the selectivity of TFM to lamprey. The sea lamprey does not have as great a capacity to detoxify TFM and thus concentrations of the chemical increase unchecked to lethal concentrations in the lamprey, whereas the mechanism of glucuronidation detoxifies the chemical in trout.

Conjugation and biliary excretion play a major role in the metabolism of several chemicals in fish (Allen et al. 1979a, b). Statham and Lech (1975) identified the major metabolite of Bayer 73 in fish as the glucuronide conjugate. Schultz and Harman (1978) also showed the glucuronide conjugate to be the major metabolite and again found high concentrations of the conjugated lampricide in gallbladder bile.

The elimination of TFM from blood (Lech 1973; Hunn and Allen 1975a) is rapid and elimination of the lampricide from muscle is usually complete within 24 h of recovery (Sills and Allen 1975). Renal excretion of TFM was shown to be a major route of elimination of the lampricide (Hunn and Allen 1975b; Allen and Hunn 1977), with ~97% of the excreted TFM in the urine in the conjugated form.

Bayer 73 is also excreted in the urine of fish (Allen et al. 1979b). Rainbow trout injected with 200 μg of Bayer 73 excreted 25% of the dose in the urine within 24 h and 20% was found in gallbladder bile. Analysis of the urine indicated that ~92% of the Bayer 73 excreted in the urine was in the form of the glucuronic acid conjugate.

SELECTIVITY

The success of the Lamprey Control Program over the last 15 yr has been due in large part, if not entirely, to the selective toxicity of TFM for the sea lamprey. While there are very few examples in the literature of chemical agents which have absolute selectivity, the more common situation encountered is a relative selective toxicity. The extent of selectivity is often manifest as a difference in concentration needed to kill the target species when compared to the concentration which is lethal to nontarget organisms. In reviewing the literature on selective toxicity of certain insecticides, one can find selectivity ratios between nontarget and target species as high as 1000 for certain pyrethroid insecticides to as low as 2 for several organochlorine insecticides.

The fact that certain chemicals do possess selective toxicity implies that there are specific biochemical or physiological differences among the species in question, and that at least one of the interactions of the chemical with these species involves a site or sites which are intimately associated with these biological differences. Broadly speaking, selectivity of chemicals among species can be divided mechanistically into two general classes. The first mechanism of selective toxicity is related to qualitative or quantitative differences between the species in the biological disposition of the chemical. These dispositional differences may be distinct from the actual toxicological or pharmacological action of the chemical, and may include differences in absorption, uptake, binding, metabolism, and excretion of the chemical between the species in question. A second mechanism of selectivity is unrelated to dispositional factors and is essentially a question of target organ sensitivity between species. In this situation, the susceptible organism is biochemically or physiologically different from the nonsusceptible organism, and the action of the toxicant is directed toward these differences. Although these two general mechanisms of selective toxicity may appear to be clear-cut, in actual practice one may find that a selective chemical may act by a combination of these two distinct mechanisms.

The search for selectively acting insecticides is never ending, and historically the approach has been through screening procedures aided by structural activity correlations. The task of the development of selectively toxic insecticides and other chemicals over the past few years has become more sophisticated as more becomes known about the basic biochemistry and physiology of the target species. Thus, it has become possible to some extent to develop chemicals based upon a structure which possesses selectivity which has been modified to provide maximum toxicity to the target species and minimum toxicity to nontarget species. Ideally, such modifications include those which provide maximum stability in the physical environment, rapid biotransformation and excretion by the nontarget organism, and a site of action specific to the target organism.

The relative selective toxicity of TFM for the sea lamprey was discovered largely through a screening program and little was known at that time of its mechanism of action or of its biological disposition among the target and nontarget species. The selectivity ratios for TFM among nontarget organisms and the sea lamprey are not remarkably high and range from 2 to 10. Studies over the past several years have provided information concerning the biological disposition of TFM in several aquatic species, and have provided some insight into the possible mechanism for its relative selective toxicity. When sea lamprey and rainbow trout fingerlings were exposed to concentrations of TFM which were lethal to the lamprey but not to the trout, the concentration of TFM found in the lamprey was observed to be much higher than that seen in the trout sampled during the same time period. On the other hand, the concentrations of the major metabolic product, TFM glucuronide, were found to be low in the lamprey but higher in rainbow trout. In several species of fish exposed to TFM, TFM glucuronide appears to be the major metabolic product and this material is rapidly excreted into the bile and urine during both exposure and depuration.

Biochemical studies using liver fractions from rainbow trout and sea lamprey have indicated that lamprey have a limited ability to conjugate TFM with glucuronic acid when compared to rainbow trout. These and other studies indicate that at least a portion of the selective toxicity of TFM for the sea lamprey may be related to the inability of the sea lamprey to conjugate and excrete TFM when compared to rainbow trout. While the lower rates of conjugation and excretion of TFM in the sea lamprey could account for the higher steady state tissue levels of TFM in the sea lamprey during exposure, differences in uptake of TFM from the surrounding water by the lamprey and rainbow trout have not been fully investigated and could be a contributory factor to selectivity. However, it is clear from the available evidence that the selectivity of TFM may be related to its biological disposition rather than a mechanism concerned with target organ sensitivity. Unpublished observations concerning this latter point indicate that the sea lamprey may be inherently less sensitive to the toxic effects of TFM than rainbow trout when equal blood and tissue concentrations in both species are considered, and had it not been for the more rapid conjugation and excretion of TFM by the trout, TFM may have turned out to be more toxic to trout than lamprey. Since the exact mechanism of toxicity of TFM for both of these species is not known, it is difficult to speculate on this point. However, if the observed uncoupling of oxidative phosphorylation by TFM is related to its toxicity (the cause of death), it is possible that the lamprey is less sensitive since there are indications that this species may be less dependent on oxidative metabolism for life functions when compared to trout. This is not unreasonable since it is documented that dependency upon anaerobic versus aerobic metabolism varies considerably among aquatic species.

DEVELOPMENT OF NEW LAMPRICIDES

Assuming that the selective toxicity among sea lamprey and rainbow trout is due at least in part to the greater rate of conjugation and elimination of TFM by rainbow trout, there may be some merit in taking advantage of this observation in the quest for new and more selective lampricides. A potentially selective compound would (1) be taken up more rapidly by the lamprey than by other nontarget aquatic species; and (2) be metabolized and eliminated more rapidly by the nontarget species than by the sea lamprey. Relatively little is known concerning the differences between the sea lamprey and other species as related to the uptake of chemicals. Experimental observations previously mentioned indicate that rainbow trout have a greater ability to conjugate and excrete TFM; it would be desirable to know if this extends to other phenolic compounds. If this phenomena holds up with other phenols, then it would seem desirable to use a chemical which has a functional group which can be conjugated with glucuronic acid or possibly sulfate.

Maximum selectivity of this hypothetical compound could be achieved if its toxicological effect could be directed towards disruption of some key process, either biochemical or physiological, in the sea lamprey which was more important for survival than in other nontarget species. It is obvious that from an experimental point of view, this facet of research would be the most difficult since relatively little is known concerning the normal biochemistry and physiology of the lamprey. However, a useful starting point may be to determine the relative contributions of anaerobic versus aerobic metabolism between sea lamprey and other aquatic species. Armed with the knowledge of ancillary pathways for the generation of metabolic energy anaerobically, one may be able to design selective chemicals which (1) are taken up more rapidly by the lamprey; (2) are metabolized and excreted by nontarget species; and (3) have functional groups which interfere with the physiological or biochemical processes of lamprey.

Allen, J. L., V. K. Dawson, and J. B. Hunn. 1979a. Biotransformation of selected chemicals by fish, p. 121–129. *In* M. A. O. Kahn, J. J. Lech, and J. J. Menn [ed.] Pesticide and xenobiotic metabolism in aquatic organisms. ACS Symposium Series 99, Washington, D.C.

1979b. Excretion of the lampricide Bayer 73 by rainbow trout, p. 52–61. *In* L. L. Marking and R. A. Kimerle [ed.] Aquatic toxicology. ASTM Spec. Tech. Publ. 667, Philadelphia, PA.

Allen, J. L., and J. B. Hunn. 1977. Renal excretion in channel catfish following injection of quinaldine sulfate or 3-trifluoromethyl-4-nitrophenol. J. Fish. Biol. 10: 473–479.

Applegate, V. C., J. H. Howell, A. E. Hall Jr., and M. A. Smith. 1957. Toxicity of 4,346 chemicals to larval lampreys and fishes. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. 207: 157 p.

Applegate, V. C., J. H. Howell, J. W. Moffett, B. G. H. Johnson, and M. A. Smith. 1961. Use of 3-trifluormethyl-4-nitrophenol as a selective sea lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 1: 35 p.

Applegate, V. C., B. G. H. Johnson, and M. A. Smith. 1966. The relation between molecular structure and biological activity among mononitrophenols containing halogens. Great Lakes Fish. Comm. Tech. Rep. 11: 1–19.

Bills, T. D., and L. L. Marking. 1976. Toxicity of 3-trifluoromethyl-4-nitrophenol(TFM), 2′-5-dichloro-4′-nitrosalicylanilide (Bayer 73) and a 98:2 mixture to fingerlings of seven fish species and to eggs and fry of Coho salmon. U.S. Fish. Wildl. Serv. Inv. Fish Control 69: 1–9.

Dawson, V. K., K. B. Cumming, and P. A. Gilderhus. 1975. Laboratory efficacy of 3-trifluoromethyl-4-nitrophenol (TFM) as a lampricide. U.S. Fish. Wildl. Serv. Inv. Fish Control 63: 13 p.

1977. Efficacy of 3-trifluoromethyl-4-nitrophenol (TFM), 2′,5-dichloro-4′-nitrosalicylanilide (Bayer 73) and a 98:2 mixture as lampricides in laboratory studies. U.S. Fish. Wildl. Serv. Inv. Fish Control 77: 11 p.

Howell, J. H., E. L. King Jr., A. J. Smith, and L. H. Hanson. 1964. Synergism of 5,2′-dichloro-4′-nitrosalicylanilide and 3-trifluormethyl-4-nitrophenol in a selective lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 8: 21 p.

Hunn, J. B. 1971. Physiological response of fish to TFM, Appendix XIV. Great Lakes Fish. Comm. Rep. Ann. Meet., Ann Arbor, MI. June 23–25, 1971. p. 14–16.

Hunn, J. B., and J. L. Allen. 1974. Movement of drugs across the gills of fishes. Annu. Rev. Pharmacol. 14: 47–55.

1975a. Residue dynamics of quinaldine and TFM in rainbow trout. Gen. Pharmacol. 6: 15–18.

1975b. Renal excretion in coho salmon (*Oncorhynchus kisutch*) after acute exposure to 3-trifluoromethyl-4-nitrophenol. J. Fish. Res. Board Can. 32: 1873–1876.

Kawatski, J. A., and J. J. McDonald. 1974. Effect of TFM (3-trifluoromethyl-4-nitrophenol) on *in vitro* tissue respiration of four species of fish with preliminary notes on its *in vitro* biotransformation. Comp. Gen. Pharmacol. 2: 15–24.

Lech, J. J. 1973. Isolation and identification of 3-trifluoromethyl-4-nitrophenol glucuronide from bile of rainbow trout exposed to 3-trifluoromethyl-4-nitrophenol. Toxicol. Appl. Pharmacol. 24: 114–124.

Lech, J. J., and N. V. Costrini. 1972. *In vitro* and *in vivo* metabolism of 3-trifluoromethyl-4-nitrophenol in rainbow trout. Comp. Gen. Pharmacol. 3: 160–166.

Lech, J. J., S. Pepple, and M. Anderson. 1973. Effect of novobiocin on the acute toxicity, metabolism and biliary excretion of 3-trifluoromethyl-4-nitrophenol in rainbow trout. Toxicol. Appl. Pharmacol. 25: 542–552.

Lech, J. J., and C. N. Statham. 1975. Role of glucuronide formation in the selective toxicity of 3-trifluoromethyl-4-nitrophenol (TFM) for the sea lamprey: comparative aspects of TFM uptake and conjugation in the sea lamprey and rainbow trout. Toxicol. Appl. Pharmacol. 31: 150–158.

LeFevre, P. G. 1972. Principles of permeation and distribution, p. 5–38. *In* P. K. Knoefel [ed.] Absorption, distribution, transformation, and excretion of drugs. Charles C. Thomas, Springfield, IL.

Marking, L. L., and J. W. Hogan. 1967. Toxicity of Bayer 73 to fish. U.S. Fish. Wildl. Serv. Inv. Fish Control 19: 10 p.

Marking, L. L., and J. W. Hogan. 1967. Toxicity of Bayer 73 to fish. U.S. Fish. Wildl. Serv. Inv. Fish Control 19: 10 p.

Marking, L. L., and L. E. Olson. 1975. Toxicity of the lampricide 3-trifluoromethyl-4-nitrophenol (TFM) to nontarget fish in static tests. U.S. Fish. Wildl. Serv. Inv. Fish Control 60: 13 p.

Meredith, R. 1971. The dependence of pH on the molluscicidal activity of the ethanolamine salt of 5,2′-dichloro-4′-nitrosalicylic aniline in solution in 10° artificial hard water. WHO/SCHISTO/71: 12: 11 p.

Schultz, D. P., and P. D. Harman. 1978. Uptake, distribution, and elimination of the lampricide 2′,5-dichloro-4′-nitro[^{14}C]salicylanilide (Bayer 2353) and its 2-aminoethanol salt (Bayer 73) by largemouth bass. J. Agric. Food Chem. 25: 226–1229.

Schultz, D. P., P. D. Harman, and C. W. Luhning. 1979. Uptake, metabolism, and elimination of the lampricide 3-trifluoromethyl-4-nitrophenol by largemouth bass (*Micropterus salmoides*). J. Agric. Food Chem. 27: 328–331.

Sills, J. B., and J. L. Allen. 1975. Accumulation and loss of residues of 3-trifluoromethyl-4-nitrophenol (TFM) in fish muscle tissue: laboratory studies. U.S. Fish. Wildl. Serv. Inv. Fish. Control 65: 10 p.

Starkey, R. J., and J. H. Howell. 1966. Substituted nitrosalicylanilides: a new class of selectively toxic sea lamprey larvicides. Great Lakes Fish. Comm. Tech. Rep. 11: 21–29.

Statham, C. N., and J. J. Lech. 1975. Metabolism of 2′,5-dichloro-4′-nitrosalicylanilide (Bayer 73) in rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 32: 515–522.

Sterility Method of Pest Control and Its Potential Role in an Integrated Sea Lamprey (*Petromyzon marinus*) Control Program[1,2]

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The sterility method of pest control could be an effective tool in the sea lamprey (*Petromyzon marinus*) control program in the Great Lakes. Some of the requirements for its successful application have been met. A field study demonstrated that the release of male sea lampreys, sterilized by the injection of 100 mg/kg of *P*,*P*-bis(1-aziridinyl)-*N*-methylphosphinothioic amide (bisazir), will reduce the number of viable larvae produced. The actual reduction in reproductive success that occurred was directly related to the ratio of sterile to normal males in the population. The technique can be used in many ways in an integrated control program and has considerable potential for the more effective control of the sea lamprey. Eradication is a distinct possibility.

Key words: sea lamprey, *Petromyzon marinus*; pest control, fish control, sterile-male technique, sterilization, chemosterilants, bisazir, Great Lakes

HANSON, L. H., AND P. J. MANION. 1980. Sterility method of pest control and its potential role in an integrated sea lamprey (*Petromyzon marinus*) control program. Can. J. Fish. Aquat. Sci. 37: 2108–2117.

La méthode de contrôle des pestes par stérilité pourrait être un outil efficace dans le contrôle de la grande lamproie marine (*Petromyzon marinus*) dans les Grands Lacs. Certaines des conditions nécessaires au succès de son application sont déjà satisfaites. Une étude sur le terrain démontre que la mise en liberté de lamproies mâles, stérilisées par injection de 100 mg/kg de *P*,*P*-bis(1-aziridinyl)-*N*-méthylphosphinothioïque amide (bisazir), réduit le nombre des larves viables produites. La diminution réelle du pouvoir reproducteur est en relation directe avec le rapport des mâles stériles à celui des mâles normaux dans la population. Cette technique peut être utilisée de bien des manières dans un programme de contrôle intégré et devrait permettre un contrôle plus efficace de la grande lamproie marine. Son éradication est même une bonne possibilité.

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THE purpose of this paper is to discuss the potential role of the sterility method of pest control in an integrated sea lamprey (*Petromyzon marinus*) control program. While selective toxicants (Applegate et al. 1961; Howell et al. 1964; Manion 1969) have successfully controlled lamprey populations in the Great Lakes by treatment of larval populations in streams, other methods of control should be considered in any pest control program. A brief history of the development of the sterile-male theory is described and the basic principles behind the theory and the requirements for its successful application are presented. A field trial designed to evaluate the effectiveness of sterilized male lampreys in reducing the reproductive potential of an isolated spawning population is described. In addition, various ways of using the technique in the sea lamprey control program are described and its potential value is examined.

Development of the Theory

The idea that sterile animals could be used to control or eradicate certain pests was first formulated by Dr E. F. Knipling in an isolated laboratory in Texas in 1937. While working on the biology and control of the screw-worm fly, *Cochliomyia hominivorax*, a serious pest of livestock, he suggested that if some way could be found to sterilize the

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males without impairing their mating ability, it might be feasible to use these sterilized males to eradicate isolated populations of this pest. Although his ideas met with considerable skepticism for several years, he felt they had considerable merit and continued to work on various mathematical models. In 1951, Bushland and Hopkins (1951) successfully sterilized screw-worms with gamma radiation and showed that the sterile-male technique actually worked in laboratory cages. Field studies on the 440 km² West Indies island of Curacao, in which the screw-worm population was eradicated in four generations (about 3 mo), demonstrated conclusively the soundness of the sterile-male technique as a method of pest control (Baumhover et al. 1955). The success of this experiment was greater than expected and soon plans were formulated to expand the project to the southeastern United States where the screw-worm fly was eventually eradicated (Knipling 1960). Eradication has not yet been achieved in the southwest because of reinfestation from Mexico, although a substantial reduction in the population has been achieved. The success of Knipling's sterility technique in eradicating or suppressing the screw-worm fly has led to its use against numerous other insect pests (La Chance et al. 1967; Weidhaas 1968; Knipling 1972).

Knipling (1959) suggested that the possibility of controlling pests by the sterile-male method is not necessarily limited to insects, but theoretically can be applied to any animal. However, only biologists familiar with the life history, habits, and population dynamics of the pest to be controlled can determine the feasibility of using the technique.

Basic Methods and Requirements for Using the Technique

BASIC METHODS

The fundamentals of population suppression by the use of sterility techniques have been thoroughly discussed by Knipling (1955, 1959, 1960, 1964, 1966, 1968). Essentially, the techniques involve two distinct procedures: (1) The mass production, sterilization, and release of fully competitive sterile organisms into a natural population. Essentially, the reproductive potential of the natural population is reduced in proportion to the ratio of sterile to fertile organisms present. For example, if the ratio is 1:1, the reproductive potential of the natural population will be reduced by 50%; and if it is 3:1, it will be reduced by 75%. (2) The sterilization of a portion of the natural population. In this method, two separate effects are produced; sterilized individuals cannot reproduce, an equivalent to killing in terms of the reproductive potential of the population; and the sterilized organisms reduce the reproductive capacity of the remaining normal individuals in the population. For example, if 90% of the population is sterilized, the effect on the reproductive potential of the population would be the same as if 90% of the organisms were killed. The sterile organisms will then reduce the reproductive potential of the remaining normal 10 by 90%, leaving 1% to reproduce (Table 1). If the natural population is sterilized, it will be necessary to sterilize both sexes. If animals are trapped, the destruction or removal of the females and return of sterile males into the environment will have the same effect as the sterilization and release of both sexes (Knipling 1968).

TABLE 1. The maximum effect on reproduction resulting from different sterility levels in natural pest populations (Knipling 1968).

Sterility level, %	Maximum reduction in reproductive potential, %
25	43.75
50	75
75	93.75
80	96
90	99
99	99.99

BASIC REQUIREMENTS

The basic requirements and the type of information needed to appraise or establish the feasibility of employing the sterile-insect-release technique were described by Knipling (1968). The feasibility of employing the sterility technique to advantage for controlling sea lampreys will be governed by essentially the same factors:

1) Development of a method of inducing sterility without serious adverse effects on the mating behavior and competitiveness of the males.

2) A practical method of obtaining large numbers of male lampreys.

3) Quantitative information on the density of the natural population.

4) A practical way of further reducing natural populations to levels manageable with sterile males may be necessary.

5) Information on the rate of population increase as a guide for determining the necessary rate of overflooding with sterile males.

6) The cost of capturing and sterilizing a portion of the natural population or rearing and releasing the required number of sterile males should be favorable in relation to costs of other methods of control.

7) If elimination cannot be achieved because of reinfestation by migrating lampreys, the cost of maintaining control by continuing sterile male releases must be favorable in relation to the costs for other available methods.

8) There could be justification for employing the sterility technique, even if the method is more costly than current ways to control or eradicate lamprey populations, if hazards to man and his environment are an important consideration when other methods of control are employed.

9) Sterile males to be released must not cause undue damage to fish that outweigh the benefits of achieving or maintaining population control.

All of these factors must be satisfied or considered in any lamprey control program involving the use of sterility techniques. Since the techniques can be used in many different ways, certain factors may be more important in some instances than in others. Once the technique is considered feasible, the actual application will require complex operations and considerable precision. Carelessness in planning and applying the technique could result in unnecessary failures.

Chemosterilization of the Sea Lamprey

The primary requirement for employing the sterility technique is the availability of a method of inducing sterility which has no serious adverse effect on the mating behavior and competitiveness of the organisms. Two methods of producing sterility in insects have been investigated most extensively; the exposure of the organism to X-rays or gamma rays from Cobalt 60 isotopes, and the use of chemicals. Many chemical compounds can destroy the reproductive capacity of insects without impairing their sexual competitiveness (Borkovec 1966; LaBrecque and Smith 1968), and therefore may be useful for more effective control or eradication of certain insect pests. In males, sterility is based on the induction of dominant lethal mutations in the sperm, inactivation of the sperm, or by aspermia. In the females, sterility can result from dominant lethal mutations in the eggs that are deposited or from infecundity. All of these types of induced sterility are potentially useful for pest control.

The recent discovery of a chemosterilant for sea lampreys offers promise for more effective control of this pest. Laboratory tests showed that an intraperitoneal injection of *P,P*-bis(1-aziridinyl)-*N*-methylphosphinothioic amide[3] (bisazir) caused sterilization of spawning-run sea lampreys (Hanson and Manion 1978). Lampreys to be sterilized were injected with bisazir (100 mg/kg) dissolved in saline (9 g NaCl/1000 mL distilled water) at the rate of 10 000 mg/L. Although sperm from sterilized males successfully fertilized eggs, complete mortality occurred before the embryos reached the larval stage (stage 18; Piavis 1961).

Field Study

A field study in 1974 on the Big Garlic River, Marquette County, Michigan (Hanson and Manion 1978), demonstrated that sterilization of lampreys with bisazir had no noticeable effect on the nest building and spawning behavior of lampreys of either sex and did not destroy the mating competitiveness of the males. A second field study was initiated in 1976 to more fully evaluate the potential effectiveness of bisazir-sterilized males in a sterile-male-release program. A known population of sterile and normal spawning-run lampreys was confined in a portion of the Big Garlic River, their behavior observed, and reproductive success determined.

THE STUDY SITE

The section of river used in this study extends from Mac's Falls upstream 2.5 km to Kreig's Falls. Each falls is a barrier to the upstream movement of sea lampreys. A downstream trap was constructed at the lower end of the study area to prevent and monitor the downstream movement of the adult sea lampreys. Two fyke nets were placed below the trap to monitor any escapement. The nets fished over 90% of the stream volume during periods of normal flow. A thermograph and staff gauge were placed in the stream to monitor the water temperature and water level. The study area has excellent spawning and larval habitat and is a known producer of sea lampreys (Manion and McLain 1971; Hanson and Manion 1978). The stream is small (average flow — 0.4 m^3/s) and the water clear, which facilitated the observations on spawning lampreys under normal conditions.

COLLECTION AND RELEASE OF LAMPREYS

Spawning-run sea lampreys were collected by hand below a power dam on the Manistique River, Lake Michigan, on May 28 and were transferred to the Hammond Bay Biological Station where they were weighed; sexed according to their external characteristics (Vladykov 1949); and marked with a Petersen tag consisting of a white, numbered disc and a colored, unnumbered disc. The colored discs were placed on the right side of the males and on the left side of the females. The color of the tag identified the sterile and normal males. In addition, normal males were marked with a small, V-shaped notch on the dorsal fin in case of tag loss. Average weights were 262 g (range 163–345 g) for normal males and 266 g (range 112–449 g) for sterile males. Females averaged 270 g (range 172–396 g). Male lampreys to be sterilized were injected intraperitoneally with bisazir (100 mg/kg) which had been dissolved in saline. Injected lampreys appeared anesthetized and were held in a closed system (150-gallon tank; aerated, but not supplied with running water) for 24 h. We believe that much of the chemosterilant was either metabolized or excreted by the lampreys since they appeared to recover fully during this period. The lampreys were removed and the water in the tank was treated with 10 mL of hydrochloric acid per 3.785 L of water. This treatment causes complete degradation within minutes of any bisazir which may be present in the water (Dr A. B. Borkovec, U.S. Department of Agriculture, Insect Reproduction Laboratory, Beltsville, MD, personal communication). The lampreys were then held for an additional 24–48 h in tanks supplied with running water to ensure their full recovery. On June 5, all lampreys were transported to the Big Garlic River and released at the upper end of the study area immediately below Kreig's Falls. Water temperatures in the tank truck and in the river were 16°C at the time of release.

The size and composition of the experimental spawning population was determined by making the following assumptions: (1) the spawning run in the Big Garlic River consisted of 1000 adult sea lampreys, all of which would attempt to spawn in the study area; (2) of the lampreys that enter the Big Garlic River to spawn 30% are males (the percentage of males taken from the electrical barriers during spawning runs in tributaries along the south shore of Lake Superior has ranged between 29 and 31 from 1971 to 1978); (3) a barrier in the river below the study area prevented 90% of the lampreys (900 lampreys) from reaching the study area; and (4) all of the 900 lampreys (270 males and 630 females) that are unable to migrate upstream past the barrier are captured; the males are sterilized and released in the study area and the females are killed.

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[3] This compound (USDA code number A13-61585) was obtained from Dr A. B. Borkovec, U.S. Department of Agriculture, Insect Reproduction Laboratory, Beltsville, MD 20705, USA.

Thus, we placed 30 normal males, 70 normal females, and 270 sterilized males in the study area. We replaced 32 of the 35 dead lampreys found in the stream, trap, or nets before June 22 with lampreys that had been held in live cages in the Chocolay River near Marquette, MI. The cause of death was not determined. The injection of bisazir did not appear to be the cause, since a higher percentage of females and normal males died than sterile males. Dead lampreys found after June 22 were not replaced because spawning had started and we had difficulty determining if they had spawned and died, or had died from other causes.

DOWNSTREAM MOVEMENT

The trap and fyke nets were checked daily. Lampreys captured alive were returned upstream to the original release point until June 28. None were returned after June 28, since spawning had been going on for nearly a week and many of the captured lampreys were spent and dying. No significant difference was observed in the downstream movement of sterile and normal males or between males and females during the study.

Many lampreys moved downstream the first 2 d (June 6–7) after their release. One hundred were captured in the trap the first day, and 28 the second day. Some escapement from the trap occurred during these 2 d as two lampreys were captured in the fyke nets. Three others were captured in the nets before spawning began, but we believe that they had by-passed the trap during the first escapement and had remained in the pool between the trap and the nets. One lamprey had been observed in this pool on several occasions before it was captured. These lampreys apparently jumped either a diversion board on the trap or the end board of the cage (200-mm jump). Modifications of the trap apparently prevented any further escapement until July 10 (after spawning was completed), when an opening was observed in the trap and two dead lampreys were captured in the nets. Examination of potential spawning areas below the study area during and after the spawning period revealed that some escapement took place past the trap and nets. One sterile male was observed on a male nest (no eggs in nest); no other lampreys were seen. Four other male nests and one nest containing eggs were found in a short section of the stream immediately below Mac's Falls. The nest building and spawning could have been accomplished by one pair of lampreys. The nest that contained eggs was included in the study. No adults were captured in the permanent, inclined-plane trap located 3.9 km below Mac's Falls (McLain and Manion 1967).

After the first 2 d downstream movement slowed considerably and only 29 adults were captured until spawning began on June 22. Movement then increased and 148 lampreys were captured in the trap during the spawning period (June 22–July 6). After spawning was completed (July 7), we captured 26 lampreys, most of which were spent and dead. The last lamprey was captured on July 14.

NEST CONSTRUCTION AND SPAWNING

The study area was surveyed daily after the adults were released and each occupied nest was marked with an aluminum-painted stone bearing a red number. Nests occupied by male and female lampreys were observed for 10 min each day and tag color (and number, if possible), sex, physical condition, and nest building or spawning of the occupants was recorded.

The first observed nest building was on June 15 when five males were observed on separate nests and 18 unoccupied nests were counted. No spawning had taken place in any of these nests as no eggs had been deposited. From June 15 through June 21, we observed 44 males and 2 females on nests. Of the 44 males, 40 (91%) were sterile. Over the entire nest building and spawning period (June 15–July 6), 377 sightings were made of males on nests. Of these, 334 (89%) were of sterile males. A total of 97 males were observed on nests with females and of these, 83 (86%) were sterile. These percentages are very close to what would normally be expected in a population consisting of 90% sterile males.

Of the 83 observations of nesting lampreys, 72 were of monogamous pairings and 11 were of polygamous groups (one male and two females). No polyandrous spawning was observed, although we did observe males fighting for nests on 17 different occasions. The fights involved 37 males, of which 33 (89%) were sterile. Two males fought for a nest in 15 instances; three fought for a nest on one occasion; and four males were observed fighting for a nest on another occasion. Water temperatures during the spawning period (June 22–July 6) varied from 10.0 to 17.2°C.

DEVELOPMENT OF EMBRYOS AND EVACUATION OF NESTS

After spawning was completed the nests were checked for the presence or absence of eggs. If the nest contained eggs, a small sample was taken, using a net and method similar to that described by Hanson and Manion (1978); preserved in 5% formalin; and embryos assigned to developmental stages based on the description by Piavis (1961). This information, along with spawning observations, was used to determine a schedule for nest excavation.

TABLE 2. Survival of sea lamprey embryos found in 74 nests in a section of the Big Garlic River where spawning sea lampreys were released June 5, 1976.

Nest observations	Number nests	Number nests with 100% mortality	Embryos			
			Dead	Alive	Total	% dead
Only sterile males observed with females	44	38	439 231	24 633	463 864	94.7
Only normal males or both sterile and normal males observed with females	11	0	70 501	53 794	124 295	56.7
No males observed with females	19	16	128 198	29 018	157 216	81.5
Total	74	54	637 930	107 445	745 375	85.6

On July 6, 7, and 8, 213 nests were checked; 101 were unmarked (no lampreys had been observed on them) and 112 were marked (at least one lamprey had been observed on each nest). Of the unmarked nests 89 did not contain eggs and apparently had been constructed and abandoned by male lampreys. The large number of male nests was probably due to the high ratio of males to females in the population. Iron ore pellets that had been painted red were placed in these nests to indicate that no eggs had been deposited. The remaining 12 nests that contained eggs were marked with an aluminum-painted rock bearing a red numeral for later identification and excavation. Of the 112 nests on which at least one lamprey had been observed, 62 contained eggs. At least one pair of lampreys was observed on 55 of these nests and either males or females (no pairs) were observed on 7.

Nests were dismantled and all eggs were removed from each of the 74 successful nests (contained eggs) about 18 d after egg deposition. This was sufficient time for the embryos in nests in which sterile males had spawned to die, and was soon enough so that eggs fertilized by normal males would not have developed far enough so that they would be able to leave the nest (stage 17). Since only stage 13, 14, and 15 embryos (Piavis 1961) were found, we had apparently excavated each nest at the proper time. The trap used to collect eggs and embryos from the nests, and the method of dismantling nests, was similar to that used by Manion (1968). The trap consisted of a rectangular plywood funnel, 500 mm wide by 180 mm high, with a 600 × 205 mm aluminum wing on either side. A 1.5 m plankton net (363 N; 30–50) was attached to the funnel. Eggs and embryos were preserved in 5% formalin, examined microscopically, counted and staged using Piavis' (1961) criteria.

NESTING OBSERVATIONS AND DEVELOPMENT OF EMBRYOS

Our observations of the spawning that took place in the 74 nests agreed closely with the success or failure of the eggs to develop (Table 2). We observed sterile males with females on 44 nests; 38 of these nests contained only dead eggs, while some developing embryos were found in 6 nests. Two of these nests were overlapped by nearby nests in which normal males were observed spawning. Presumably the live embryos came from these nests. Normal males could have spawned in the other four nests unobserved since each nest was only observed for about 10 min or less each day.

All nests (11) in which only normal males or both normal and sterile males were observed with females contained developing embryos. Apparently normal and sterile males had both spawned in many of these nests, since it was not unusual to find a group of developing embryos in one portion of a nest and a group of dead embryos in another.

In the remaining 19 nests, no lampreys were observed in 12 nests while males or females were observed on 7 nests, but never both at the same time. We found only dead eggs in 16 nests, while developing embryos were found in 3.

ESTIMATED REDUCTION IN REPRODUCTIVE POTENTIAL

A total of 54 (73%) of the 74 nests contained only dead eggs or embryos. The large variability in the number of embryos in the nests (range 103–34 310) and the fact that several nests were spawned in more than once by different pairs at different times and some were spawned in by both sterile and normal males, would not permit a reliable estimate of the actual reduction in reproductive potential that occurred.

Our observations showed that 89% of the males fighting for nests, 89% of the males on all nests, and 86% of the males on nests with females were sterile. Since 90% of the males in the study area were sterile, they were essentially fully competitive for nests and spawning partners. Therefore, nearly 90% of the spawning acts should have been between sterile males and females and almost 90% of the eggs should have been fertilized by sperm from sterile males. Nest excavations revealed that 637 930 (86%) of the 745 375 embryos were dead. The percentage of unfertilized eggs and the natural mortality rate of developing embryos found in the nests is not known, although it is believed to be something less than 15%, based on counts from selected nests during the field studies and from Manion's (1968) work. A 15% natural mortality rate (111 806) would reduce the number killed by bisazir to 526 124 among embryos that would normally have been alive (633 569), and the bisazir-induced mortality rate would be 83%. Thus, the actual reduction in reproductive potential that occurred was very close to that expected.

The field study demonstrated conclusively that the release of bisazir-sterilized male lampreys into a spawning population of lampreys will reduce the number of viable larvae that would normally have been produced, and that the actual reduction in reproductive potential that will occur in any sterile-male-release program using bisazir-sterilized males will be directly dependent upon the ratio of sterile to normal males present in the population.

Potential Role of Sterility Method in an Integrated Sea Lamprey Control Program

Sterilization of adult spawning-run male lampreys appears to be the most practical method of getting suitable numbers of sterile animals into the spawning populations at the present time. They have completed the parasitic phase of their life cycle and their release will have no effect on fish populations. Natural mortality has had its maximum effect at this time and the release of a given number of sterile males will have its greatest effect.

SOURCE OF SPAWNING-RUN MALES

Early efforts to control sea lampreys in the Great Lakes involved the use of mechanical and electrical barriers on streams to capture spawning-run adults and prevent them from reaching the spawning grounds (McLain et al. 1965). At the present time, electric barriers are being operated in eight tributaries of Lake Superior. According to Smith et al. (1974), the number of lamprey-producing streams in Lake Superior has been reduced from 119 to about 85. Therefore, we have electric barriers on nearly 10% of these streams. These eight streams were chosen because they normally had good runs of spawning adults each spring and would be good indicators of relative abundance. Assuming these weirs are capable of capturing 10% of the adult run in Lake Superior, the destruction of the captured females, combined with the sterilization and release of the captured males, will result in a 19% reduction in the production of larvae in Lake Superior streams.

Another source of lampreys to sterilize could be from portable assessment traps fished on selected streams. In the spring of 1978, 54 traps fished on 37 tributary rivers of 4 of the Great Lakes captured 20 641 sea lampreys (J. W. Heinrich, U.S. Fish and Wildlife Service, Marquette Biological Station, Marquette, MI, personal communication). The traps captured 1003 lampreys in Lake Superior; 11 240 in Lake Michigan; 7677 in Lake Huron; and 721 in Lake Ontario. Three rivers on the north shore of Lake Michigan (Manistique River — 5408, Menominee River — 1840, and Peshtigo River —2360), and two in Lake Huron (Cheboygan River — 6489 and St. Marys River — 1148) attracted large numbers of adult lampreys and a total of 17 245 were captured. It is evident that spawning-run lampreys are attracted to the larger streams and it is becoming increasingly apparent that we can capture a large portion of the spawning population by increasing the trapping effort and improving the design of the trapping devices on only a relatively few streams.

PROBLEM STREAMS

Many chemical treatments of streams are less than 100% effective (Manion 1969; Smith et al. 1974) — particularly those made in several of the larger, more complex systems which have beaver ponds, lakes, oxbows, large deltas, or other areas which are difficult to treat. Theoretically, if a stream contained a population of 100 000 larvae and the chemical treatment was 99% successful, 1000 potential adults would survive. However, if 90% of the adults were captured at a barrier dam or electrical barrier located below the spawning grounds the reproductive potential would be reduced by 90%. If the captured females were destroyed and the males sterilized and released upstream to compete with normal males for females, the maximum reduction in reproductive potential would be 99% (Table 1). The population of larvae in the stream would be 1000 instead of 100 000 and the number of survivors of the chemical treatment (99% effective) would be 10 instead of 1000. Similarly, if we were deprived of the use of toxic chemicals, the establishment of a system of efficient electric barriers or barrier dams on sea lamprey producing streams, combined with the sterilization and release of the captured males, could result in a significant reduction in the reproductive potential of the entire spawning population. The reduction in the reproductive potential that occurred would depend upon the sterility level in the population which would be determined by the efficiency of the trapping system. Although these examples are hypothetical, they show the potential value of integrating different methods of control.

ST. MARYS RIVER

The St. Marys River carries the entire outflow of Lake Superior into Lake Huron. The large volume of flow in the river (average of about 2100 m^3/s) makes it unfeasible to treat the river with selective toxicants. Surveys utilizing an effective bottom toxicant to determine the distribution of sea lamprey larvae in the river have pointed to this system as a greater potential contributor to adult populations than previously recognized and may explain the difficulty of obtaining adequate control of sea lampreys in Lake Huron (Braem et al. 1978). Little is known regarding the effects of density-dependent factors, such as food and space, on the larval population in the river. If the larval population has reached its maximum potential based on these factors, the release of sterile males may have little effect unless the spawning population is greatly reduced or the ratio of sterile to normal males is high enough to cause a reduction in the larval population. If the number of spawning adults determines larval numbers, the sterility technique could be very effective.

Population estimates of adults in the St. Marys River during 1977 and 1978 indicated that the spawning run consisted of less than 10 000 adults each year (J. W. Heinrich personal communication). If means of capturing a large proportion of the spawning run in the river can be developed, this will be more effective than capturing males from other streams and using them in a sterile-male-release program. For instance, assuming a spawning population of 10 000 adults in the St. Marys River of which 50% are males, it would be necessary to capture 5000 lampreys from the river, destroy the 2500 captured females and sterilize and release the 2500 captured males to effect a 75% reduction in the reproductive potential. Destruction of the 2500 females would reduce the reproductive potential of the population by 50% and the sterilization and release of the 2500 captured males into the remaining population of 2500 males and 2500 females would reduce the reproductive potential an additional 25%, since theoretically only 1250 females would spawn with fertile males. If all male lampreys to be sterilized were captured in other streams, it would be necessary to capture and release 15 000 sterile males in the St. Marys River to effect a 75% reduction in the reproductive potential. Thus, the importance of devising effective methods of capturing adults in the St. Marys River is apparent. Utilizing males from both sources would be the most effective method of reducing the reproductive potential of the population. The capture, sterilization and release of 50% of the males in the St. Marys River, combined with the release of 15 000 sterile males from other sources, would reduce the reproductive potential of the 2500 females remaining in the river by 88%.

LAKE SUPERIOR

The buildup and eventual control of the sea lamprey population in Lake Superior from 1953 to 1970 has been thoroughly documented by Smith et al. (1974). The first confirmed record of a sea lamprey in Lake Superior occurred in 1938 (Smith and Tibbles 1980). Serious efforts to control the parasite began in 1953 with the installation of electrical barriers designed to capture and prevent sexually mature lampreys from reaching the spawning grounds (McLain et al. 1965). The highest catch was recorded in 1961 (after 3 yr of chemical treatments of streams) when 71 081 were taken at 37 barriers. An 86% reduction in the catch at these barriers in 1962 left little doubt as to the effect of the treatments and the ultimate success of control (Smith et al. 1974).

Estimates of the total spawning population in Lake Superior for each year from 1954 to 1969 were calculated by Smith (1971) by projecting the average catch per stream at index barriers to the total number of streams in which sea lampreys have spawned. The population reached its lowest level in 1967 when it was estimated to be 18 600 adults. Lamprey abundance gradually increased in subsequent years and Smith et al. (1974) stated that the increase was directly attributed to the extension of the control program to the other Great Lakes without a substantial increase in funds and staff to carry out the additional work. Intensified control measures have since reduced the numbers of lampreys taken at electric barriers to numbers comparable with that in 1967, an indication that it may be possible to reduce the spawning population to less than 20 000 lampreys through the use of selective toxicants alone.

Smith (1971) found that as the numbers of adult sea lampreys have declined, so also has the number of ammocoetes and the number of lamprey-producing streams. He also suggested that when larval populations are reduced to low numbers by chemical treatment or isolation above barriers, the size of metamorphosing individuals tends to increase and a disproportionate number of females develop. Lamprey abundance reached a peak in 1961 and the predominance of males was greatest in 1960–62, when it reached 68.2–69.6% (Smith 1971). As the lamprey population decreased, the percentages of males in the population also decreased until 1969 when it was only 26.7% (Smith 1971). A stabilization of the sex ratio has apparently occurred, since the percentage of males has only varied between 29 and 31 from 1971 to 1978 (Braem and Purvis 1978).

If we can assume that present control methods can hold the numbers of spawning-run adults to 20,000 and that the sex ratio will remain at about 30% males, the effect of various ratios of sterile to fertile males on the production of ammocoetes is readily apparent (Table 3). In this instance, population density regulating factors are ignored. It seems logical to assume that chemical treatments have already reduced the ammocoete populations to a point where density-dependent factors, such as food and space, are not a controlling factor and that any further reduction in the ammocoete population will be directly reflected in the number of metamorphosed lampreys that enter the lake. Also, since the number of parasitic lampreys is down and the numbers of prey fish are high in the lake, it seems likely that density-dependent factors are relatively unimportant during the parasitic phase of their life cycle. If these assumptions are correct, then it is evident that the release of sterile males in Lake Superior will have a direct effect on the number of spawning adults in future years. The sustained release of a constant number of sterile males will achieve a progressively higher ratio of sterile to fertile males and, therefore, become more efficient (Table 4). This ex-

TABLE 3. Potential production estimates of sea lamprey ammocoetes from a spawning population of 20 000 adults having a sex ratio which is 30% males that is subjected to various numbers of sterile males.

Ratio of sterile to fertile males	Number of sterile males	Number of fertile males	Percentage of females mated to sterile males	Number of females mated to fertile males	Number ammocoetes produced[a] (millions)
0:1	0	6000	0	14 000	45.4
0.5:1	3 000	6000	33	9 333	28.2
1:1	6 000	6000	50	7 000	22.7
2:1	12 000	6000	67	4 667	15.1
3:1	18 000	6000	75	3 500	11.3
4:1	24 000	6000	80	2 800	9.1

[a] Assume that each female spawned successfully and the mean number of larvae produced in each nest was 3240 (Manion 1968).

TABLE 4. Theoretical trend of a hypothetical lamprey population subjected to control by the release of sterile males for five generations. Assume stable spawning population of 20 000, of which 30% are males.

Assumed natural spawning population per year each generation		Number of sterile males released per year each generation	Ratio of sterile to fertile males competing for each female	Percentage of females mated to sterile males	Theoretical number spawning adults produced	
Males	Females				Males	Females
6000	14 000	6000	1:1	50.0	3000	7000
3000	7 000	6000	2:1	66.7	1000	2333
1000	2 333	6000	6:1	85.7	143	334
143	334	6000	42:1	97.6	3	8
3	8	6000	2000:1	99.95	<1	<1

ample assumes that the sterile males will come from streams tributary to the other Great Lakes.

The selective release of sterile males only in certain areas will also enhance the effects of such a program. It will not be necessary to release them in streams that are not suitable for sea lamprey production, nor will it be essential to release them in streams in which the chemical treatments are essentially totally effective. Their ultimate use, therefore, will be in streams or areas that contain, or are suspected to contain, residual populations. If this method of release is used, care must be taken not to miss any potential source of lampreys.

OTHER GREAT LAKES

If a fully integrated control program became successful in Lake Superior it may become desirable to employ the sterility technique in the other Great Lakes. Lamprey numbers in Lake Erie are so low at the present time that the release of only a relatively small number of sterile males may effectively decimate the population. It could become increasingly difficult to obtain sufficient numbers of lampreys to sterilize and release as the populations decline in Lakes Michigan and Huron. Improvements in trapping operations on rivers with large spawning runs would become necessary and the successful research and development of an attractant, most likely a sex pheromone, would be helpful. If lamprey numbers were reduced to a point where they were quite rare, it would become advantageous to search for other sources of lampreys to sterilize. Spawning-run males from Lake Ontario, or anadromous sea lampreys from Atlantic drainages of North America, are potential sources. For example, a total of 32 053 sea lamprey were lifted by the Holyoke Dam fishlift on the Connecticut River in 1976 (Foote 1976).

Although unlikely because of registration problems, it may be possible to develop a safe, effective chemosterilant and apply it in a manner similar to that presenty used in applying the selective toxicants. If the method of producing sterility and eradicating larvae in a stream are equally efficient, the potential advantage of the sterility system over the conventional system of eradication is obvious (Table 1). The use of a chemosterilant could reduce the lamprey population by 99% compared to the approximately 90% expected reduction with conventional toxicants. It is assumed that there are no adverse effects on mating behavior or length of life and that both sexes are sterilized. Any system of sterilizing members of a natural population that renders only males sterile, or only the females sterile, is not as effective as when the sterilizing agent renders both sexes sterile. A major drawback to this method of population control would be a temporary increase in the numbers of parasitic lampreys since it is essential that the sterilized larvae complete the parasitic phase of their life cycle and return as spawning adults.

Rather than treat all lamprey-producing streams with a chemosterilant and suffer the consequences of vastly increased parasitism on the fish, we could set aside one or two streams with fully effective barrier dams or electrical barriers and sterilize the larval lampreys in these streams. Production of sterilized lampreys from these streams would have to be high enough to create a sufficiently high ratio of sterile to fertile lampreys in the lakes to cause a decline in the natural population. There would be increased parasitism on fish for a number of years, but not as drastic an increase as you would have if you treated all the streams with a chemosterilant. All other lamprey-producing streams would have to be treated with lamprey toxicants to keep the natural population as low as possible.

If a developed chemosterilant is not sufficiently selective to permit safe use when applied to the lampreys in the stream in the same way selective toxicants are now employed, it may be possible to mass produce larvae in the laboratory and sterilize and release them into a "nursery" stream. The stream would be treated with a larvicide prior to the introduction of the sterilized larvae and have an effective barrier dam or electrical barrier system below the spawning grounds to prevent the reintroduction of an unsterilized population of larvae. This appears to be the most promising method of obtaining the suitable numbers of sterile animals once the natural population has been reduced to a very low number. Culture methods have been developed (Hanson et al. 1974) and mass production techniques undoubtedly could be perfected. Development of a monosex culture of all males would greatly reduce the number that would have to be produced and released and the subsequent parasitism on fish populations would be reduced by about 50%.

Discussion

Eradication is a word that is generally not used very often by people connected with the sea lamprey control program in the Great Lakes. Selective toxicants have reduced the numbers of the parasite to a level where it is evident that a reestablishment of a fisheries equal to or greater than what it was in prelamprey days will occur. Comments such as "eliminating the sea lamprey is not feasible" or "do we have enough control now?" are common. Knipling (1964) described the trend of a theoretical insect population subjected to control by insecticides. When the level of kill was 90% each generation and the rate of increase of the survivors was fivefold the net effect was to reduce the population by half. His model began with 1 000 000 insects and did not achieve zero population level until treatments had continued for 18 generations. Smith (1971) stated that "... as the number of adult sea lampreys have been reduced, the number of ammocoetes and the number of lamprey-producing streams have also declined." If we can assume that the spawning and larval habitats and larval distribution remains essentially the same, continuous application of larvicides at the same rate should result in lower and lower population levels. Zero population level may not be reached unless migration from other areas can be prevented and then may not be reached for several hundred years because of the long period of time required for each generation. The potential is there, however, and should be recognized. It will be necessary that control efforts be maintained at a constant level and will require increased vigilance by survey crews who are responsible for scheduling stream treatments. The chemical treatments which were so highly successful in terms of numbers of larval lampreys killed when the population was high are becoming increasingly inefficient in numbers killed as larval populations decrease. It will become increasingly difficult to locate these larval populations. Eventually, it will require as much effort to kill the last lamprey as it did for the original treatments of all lamprey-producing streams combined. Therefore, it is apparent that we need to develop control techniques that are more effective when the population is low.

The chemical treatments of streams have reduced the natural population to a level where sterility techniques may be practical. The development of improved methods of capturing spawning-run lampreys, combined with the subsequent release of sterilized males, will reduce the larval population at an accelerated rate. Possibly the population can be reduced to a level low enough so that the mass production and continued release of a certain number of sterile males will be capable of causing a reduction in the population. This technique has just the opposite effect of stream treatments; it is an inefficient method when natural populations are high, but becomes highly efficient when the natural population is low (Table 4). Thus, the opportunity exists to combine two contrasting systems into a more effective control or eradication program. Applegate and Moffett (1955) suggested that the most vulnerable times in the lamprey's life are its periods in a stream, either as a larvae or when it comes back to spawn. Attacking the pest at both stages should result in better control and could have a synergistic effect that may result in eradication.

Applegate and Moffett (1955) stated: "Complete eradication of sea lampreys from the Great Lakes above Niagara Falls is our objective. It may prove to be a long operation, as difficult as the campaign sometimes necessary to stamp out an agricultural or forest pest, but we are confident that we shall ultimately succeed." It is unlikely that eradication will become a reality in our lifetime, but we feel it is something worth striving for. The alternative (other than cessation of all control efforts) would be to continue the control program forever, and that's a long, long time!

The need for thorough studies of the biology, behavior, and population dynamics of sea lampreys must be stressed. Information on population densities, particularly during the parasitic and spawning phases of their life cycle, are necessary to fully evaluate the potential of the technique and to assist us in applying the technique in the most effective manner.

Applegate, V. C., J. H. Howell, J. W. Moffett, B. G. H. Johnson, and M. A. Smith. 1961. Use of 3-trifluormethyl-4-nitrophenol as a selective sea lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 1: 35 p.

Applegate, V. C., and J. W. Moffett. 1955. The sea lamprey. Sci. Am. 192: 36–41.

Baumhover, A. H., A. J. Graham, B. A. Bitter, D. E. Hopkins, W. D. New, F. H. Dudley, and R. C. Bushland. 1955. Screw-worm control through release of sterilized flies. J. Econ. Entomol. 48: 462–466.

Borkovec, A. B. 1966. Insect chemosterilants. Wiley—Interscience, New York, NY. 143 p.

Braem, R., B. G. H. Johnson, R. Schuldt, and J. J. Tibbles. 1978. Joint U.S.–Canada progress report on the status of St. Marys River sea lamprey populations. Report of Interim Meeting, November 1978. Great Lakes Fish. Comm., Ann Arbor, Agenda Item 8-C, 11 p.

Braem, R. A., and H. A. Purvis. 1978. Interim report on sea lamprey control to Great Lakes Fishery Commission. Report of Interim Meeting, November 1978. Great Lakes Fish. Comm., Ann Arbor, Agenda Item 8.B, 17 p.

Bushland, R. C., and D. E. Hopkins. 1951. Experiments with screw-worm flies sterilized by X-rays. J. Econ. Entomol. 44: 725–731.

Foote, P. S. 1976. Blood lactic acid levels and mortality of American shad (*Alosa sapidissima*) utilizing the Holyoke Dam fishlift, Massachusetts, 1974 and 1975. Presented at the workshop on American shad, December 14–16, 1976. Campus Center-Univ. of Mass., Amherst, Mass. 28 p.

Hanson, L. H., E. L. King jr., J. H. Howell, and A. J. Smith. 1974. A culture method for sea lamprey larvae. Prog. Fish-Cult. 36: 122–128.

Hanson, L. H., and P. J. Manion. 1978. Chemosterilization of the sea lamprey (*Petromyzon marinus*). Great Lakes Fish. Comm. Tech. Rep. 29: 15 p.

Howell, J. H., E. L. King jr., A. J. Smith, and L. H. Hanson. 1964. Synergism of 5,2′-dichloro-4′-nitro-salicylanilide and 3-trifluormethyl-4-nitrophenol in a selective lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 8: 21 p.

Knipling, E. F. 1955. Possibilities of insect control or eradication through the use of sexually sterile males. J. Econ. Entomol. 48: 459–462.

1959. Sterile-male method of population control. Science 130(3380): 902–904.

1960. The eradication of the screw-worm fly. Sci. Am. 203: 54–61.

1964. The potential role of the sterility method for insect population control with special reference to combining this method with conventional methods. U.S. Dep. Agric. Res. Serv. ARS-33-98: 54 p.

1966. Some basic principles in insect population suppression. Bull. Entomol. Soc. Am. 12: 7–15.

1968. The potential role of sterility for pest control, p. 7–40. *In* G. C. LaBrecque and C. N. Smith [ed.] Principles of insect chemosterilization. Appleton-Century-Crofts, New York, NY.

1972. Sterilization and other genetic techniques, p. 272–287. *In* Pest control strategies for the future. National Academy of Sciences, Washington, D.C.

LaBrecque, G. C., and C. N. Smith [ed.]. 1968. Principles of insect chemosterilization. Appleton-Century-Crofts, New York, NY. 354 p.

La Chance, L. E., C. H. Schmidt, and R. C. Bushland. 1967. Radiation-induced sterilization, p. 147–196. *In* W. W. Kilgore and R. L. Doutt [ed.] Pest control — biological, physical, and selected chemical methods. Academic Press, New York and London.

Manion, P. J. 1968. Production of sea lamprey larvae from nests in two Lake Superior streams. Trans. Am. Fish. Soc. 97: 484–486.

1969. Evaluation of lamprey larvicides in the Big Garlic River and Saux Head Lake. J. Fish. Res. Board Can. 26: 3077–3082.

Manion, P. J., and A. L. McLain. 1971. Biology of larval sea lampreys (*Petromyzon marinus*) of the 1960 year class, isolated in the Big Garlic River, Michigan, 1960–65. Great Lakes Fish. Comm. Tech. Rep. 16: 35 p.

McLain, A. L., and P. J. Manion. 1967. An all-season trap for downstream migrating fish and other aquatic organisms. Prog. Fish-Cult. 29: 114–117.

McLain, A. L., B. R. Smith, and H. H. Moore. 1965. Experimental control of sea lampreys with electricity on the south shore of Lake Superior, 1953–1960. Great Lakes Fish. Comm. Tech. Rep. 10: 48 p.

Piavis, G. W. 1961. Embryological stages in the sea lamprey and effects of temperature on development. U.S. Fish Wildl. Serv. Fish. Bull. 61: 111–143.

Smith, B. R. 1971. Sea lampreys in the Great Lakes of North America, p. 207–247. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys, Vol. I. Academic Press, New York and London.

Smith, B. R., and J. J. Tibbles. 1980. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936–78. Can. J. Fish. Aquat. Sci. 37: 1780–1801.

Smith, B. R., J. J. Tibbles, and B. G. H. Johnson. 1974. Control of the sea lamprey (*Petromyzon marinus*) in Lake Superior, 1953–70. Great Lakes Fish. Comm. Tech. Rep. 26 60 p.

Vladykov, V. D. 1949. Quebec lampreys. I.—List of species and their economical importance. Dep. Fish., Province of Quebec, Contrib. 26: 67 p.

Weidhaas, D. E. 1968. Field development and evaluation of chemosterilants, p. 275–314. *In* G. C. LaBrecque and C. N. Smith [ed.] Principles of insect chemosterilization. Appleton-Century-Crofts, New York, NY.

Role of Physical Barriers in the Control of Sea Lamprey (*Petromyzon marinus*)[1]

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Mechanical and electromechanical barriers played a significant role in the initial attempts to control sea lamprey (*Petromyzon marinus*) populations in the upper Great Lakes. More recently electromechanical weirs have been used to assess the relative abundance of spawning-run sea lampreys in Lake Superior. Development of an integrated control approach to sea lamprey control has stimulated an ongoing research program to define structural and/or velocity criteria that can be used to design barrier dams that block spawning runs of sea lamprey.

Key words: sea lamprey, *Petromyzon marinus*; physical barriers, burst swimming speed, barrier dam criteria

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Lors des premiers essais de contrôle des populations de grandes lamproies marines (*Petromyzon marinus*) dans la partie supérieure des Grands Lacs, les barrières mécaniques et électromécaniques ont joué un rôle important. On utilisa par la suite des parcs électromécaniques dans le but d'évaluer l'abondance relative des remontées reproductrices de grandes lamproies marines dans le lac Supérieur. La mise au point d'une approche intégrée du contrôle de la grande lamproie marine a stimulé un programme de recherche destiné à définir les critères de structure et de vélocité qui pourraient être utilisés dans la conception de barrages capables de bloquer les remontées reproductrices de grandes lamproies marines.

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INTEGRATED control is a pest management concept that utilizes all suitable techniques either to reduce pest populations and maintain them at levels below those causing economic injury or to so manipulate the populations that they are prevented from causing such damage (Smith and van den Bosch 1967). Physical controls, as an element of an integrated control program for pest fishes, have been used little in the history of fish management (Lennon 1970). Physical controls, however, played a major role early in the effort to control sea lamprey, *Petromyzon marinus*, in the Great Lakes, but were relegated to a minor role once selective chemical control was available.

Placement of physical barriers without regard to passage of desirable anadromous fishes has caused unaccountable damage to many major fisheries as, for example, impassable dams on salmon streams. Also, barrier dams have been used in conjunction with lake reclamation. Most important aspects in fishery work seem to be oriented toward efforts to overcome barriers to fish migrations. By implication, physical barriers could be useful in control of sea lampreys if desirable species were not impeded. The types of physical barriers used in the sea lamprey control program for the Great Lakes have evolved from simple mechanical or screen-type weirs to electromechanical weirs and finally to the development of man-made barrier dams. We will review the historical evolution of the weirs and their role in controlling populations of adult spawning-run sea lamprey and the developing rationale and criteria for barrier dams in today's sea lamprey control program.

Mechanical Control Devices (1947–52)

Applegate and Smith (1951a) describe four types of mechanical control devices that were developed for reducing the populations of sea lamprey in the upper

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Great Lakes: (1) large, permanent weirs and traps, (2) portable-type screen weirs and traps for medium- and small-sized streams, (3) barrier dams, and (4) dams and inclined-screen traps. Structures (1) through (3) were used to capture adults on the spawning runs or blocked them from reaching the spawning grounds; the inclined-screen traps destroyed young, recently transformed sea lampreys on their way downstream to the Great Lakes (Applegate 1950; Applegate and Smith 1951a; Applegate and Brynildson 1952; Applegate et al. 1952b). The structures were used to (1) immediately institute a systematic measure of sea lamprey control that would provide information on problems and costs of a large-scale control program, (2) determine whether prevention of reproduction by sea lampreys in a limited area would benefit local fish stocks, (3) continue the development and testing of improvements in design and construction of control devices, and (4) provide sites where adequate checking devices were present for testing other equipment and methods (Smith 1971).

Screen-type mechanical weirs and traps did afford some measure of control in certain streams, but were expensive to build, operate, and maintain. Early accounts of the construction and operation of the Carp Creek weir and trap by Applegate (1950), for example, showed that the use of a ½-in. (1 in. = 25.4 mm) mesh hardware cloth was effective in preventing passage of migrating adult lamprey, but much of the screen had to be inspected at frequent intervals to prevent lamprey escapement. Also, frequent cleaning of debris from the screen was necessary to prevent the damming action caused by clogged screens. In other streams, the weirs of this type were difficult to maintain in periods of ice breakup and floods so that failures were frequent and uncontrollable. An early evaluation of the various types of mechanical control devices is given by Applegate and Smith (1951a) as well as detailed diagramatic plans and descriptions of the devices.

Electromechanical Barriers (1951–79)

In an attempt to overcome the deficiencies of mechanical barriers, experiments were begun in 1951 to develop an electrical field for use with a mechanical trap. Applegate et al. (1952a) describe a simple, alternating current (AC) electrical field for use in electromechanical weirs and traps.

Electrical barriers of three types (Erkkila et al. 1956) were placed in 10 tributaries of Lake Superior in 1953 (McLain et al. 1965). Basically, they consisted of an electrode array which established an electric field across the stream. The Type A barrier had two parallel rows of hanging electrodes suspended across the stream by a catenary cable and was installed in deep, soft-bottomed streams. Type B consisted of a single row of suspended electrodes and a horizontal submerged electrode parallel to the suspended electrodes and was used in streams having moderate depths, relatively firm bottoms, and relatively fast water velocities. Type C barriers, installed in shallow, rapid-flowing streams, consisted of two horizontal submerged electrodes lying parallel across the stream bed. All installations were energized by 110-V, 60-cycle, alternating current.

Traps were installed with the wings or leads terminating at the downstream fringe of the electric field. It was believed that many fish migrating upstream would be diverted by the fringe of the electric field and in their search for a passage would enter the trap. Thus, the traps interrupted the electric fields and served as part of the barrier in the early structures. Unfortunately, the ability of sea lampreys to withstand a relatively severe electric shock without apparent physical harm, and their persistence in migrating upstream frequently enabled them to find passages which existed or developed under or around the traps. By 1956, most barriers were modified to establish an uninterrupted field from one bank to the other. The traps were installed downstream from the electric field, usually adjacent to a stream bank.

Further modifications of the AC electrical devices were required as a result of excessive mortality by electrocution of migrating fishes (Erkkila et al. 1956). Preliminary studies by McLain and Nielsen (1953) indicated that pulsated direct current (DC) could be used to direct fish movement before the fish encounter the AC electrodes and thereby reduce mortalities. During 1956, field studies were conducted in the Chocolay and Silver Rivers, tributaries of Lake Superior, to assess the efficiency of the DC diversion devices (McLain 1957; McLain et al. 1965) which were used in conjunction with the AC barrier to divert migratory fishes and sea lampreys into traps. The operation of the DC devices greatly reduced, but did not eliminate, the mortality of fish migrating upstream in the Chocolay and Silver rivers. Problems involved in the persistent fish mortality are reviewed by McLain (1957).

The influence of the electrical barriers, operated on Lake Superior from 1953 to 1960, on the sea lamprey populations in Lake Superior cannot be evaluated accurately (McLain et al. 1965). Most of the barriers were not operated long enough to reduce the contribution of sea lamprey from those streams monitored. In addition, a complete system of efficient electric barriers was never realized. However, the catch data obtained during the operation of the electromechanical weirs (16 index barriers) did provide a means of assessing the relative abundance of adult sea lamprey over a period of years (Smith 1971; Smith et al. 1974). From 1971 to 1979, only 8 of the original 16 barriers have been operated on tributaries to Lake Superior.

Barrier Dams

Barriers, natural and man-made, limit the number of streams used by spawning sea lampreys or restrict the potential spawning area within a river system.

TABLE 1. Physical criteria for sea lamprey barriers derived from studies or from consensus by investigators.

Source	Recommended height (cm)	Overhanging lip	Comments
Applegate and Smith (1951a)	79	Yes	Black River, Mackinaw Co., MI
Wigley (1959)	46–61	Yes	
Stauffer (1964)	61–66	Yes	Personal communication (1978)
Task Force	46	Yes 15–30 cm	Design criteria for 10-yr flood, D. E. Reynolds, personal communication (1978)
Tibbles	46–61	Yes	Fisheries and Oceans Canada, Sault St. Marie, Ont., personal communication (1978)

Therefore, the Great Lakes Fishery Commission (GLFC) has endorsed the installation of barrier dams as part of an integrated control program (Policy Statement of the GLFC adopted December 1, 1975, and Guidelines for Barrier Dam Program for Sea Lamprey Control, June 16, 1977; for details see U.S. Department of the Interior 1978).

On the United States side of the Great Lakes, sea lampreys spawn successfully in about 266 of the 3171 tributaries. Of these, about 124 are possible candidates for the barrier dam program. On the Canadian side of the lakes, five streams each on lakes Superior, Huron, and Ontario have been chosen as sites for installation of barrier dams (T. McAuley, Department of Fisheries and Oceans, Sault Ste. Marie, Ontario, Canada, personal communication).

Potential benefits to be derived from the installation of barrier dams include (1) more efficient control on streams where physical characteristics make lampricide treatment difficult, expensive, or ineffective; (2) savings in time and manpower and related costs through a reduction in stream miles requiring periodic lampricide treatment; (3) reduced dependency on chemicals; (4) reduced lampricide purchases in the face of rising costs and a potentially limited supply; (5) reduced quantity of lampricides added to the environment; and (6) restoration and/or survival of nontarget species in some streams.

Adverse impacts of the program may involve the following: (1) during construction, minor damage to soil and vegetative cover can be anticipated as well as increased turbidity in the stream; (2) blockage of some nontarget fish-spawning migrations, particularly rainbow smelt (*Osmerus mordax*) and suckers (*Catostomus* sp.); (3) dispersion of blocked spawning-run lamprey to other streams (Applegate and Smith 1951b); (4) impairment of the aesthetics of the dam site; (5) disruption of canoe and boat passage; and (6) creation of impoundments behind barriers.

Although some barrier dams have been built, there are few detailed experimental studies on which to base the criteria for their design. Field observations by Applegate (1950) and others have provided no precise standards as to what constitutes a barrier. Wigley (1959) has described a "partial-barrier" dam at the Cayuga Inlet in New York State. This particular structure had a drop of about 30 cm (1 ft); however, to reduce greatly or to stop migration, Wigley (1959) recommended a head (drop) of 45–60 cm. The first experimental barrier dam and its operation on the Black River in Michigan (Applegate and Smith 1951a; Stauffer 1964) indicated that a minimum head of 60 cm with an overhanging lip is necessary to provide a barrier to spawning-run sea lamprey in the Great Lakes. Other experience also indicates that an overhanging lip should be incorporated into the design of the barrier (Table 1).

More recently, W. D. Youngs (Great Lakes Fish. Comm., 1979, unpublished data) has shown that under certain experimental conditions a drop of 30 cm (weir crest to pool surface) constitutes an effective barrier to spawning migrations of Cayuga Lake sea lamprey. His experiments were conducted at the New York State Department of Environmental Conservation experimental spawning channel at Myers Point, Cayuga Lake, New York (Webster and Otis 1973) during the summers of 1978 and 1979 and demonstrated that the sea lampreys in Cayuga Lake cannot pass a vertical barrier of 30 cm or greater in height. No lamprey successfully passed this height during experiments with some 3000 lampreys. Only 16 lampreys were successful in moving upstream over barriers of 16.4 cm and greater (1978 experiments). Lamprey size was not demonstrated to be a factor in the 1979 trials, although some 1978 trials suggested that larger lampreys were the ones passing the barriers. However, the lampreys in 1979 were significantly larger than those used in the 1978 tests, but the 30-cm height remained a barrier. The sea lampreys averaged 47.05 and 46.02 cm for male and female, respectively, as compared to 44.05 and 43.36 cm for male and female lampreys, respectively, in 1978.

Although there have been few studies (see Table 1) done specifically to determine design criteria for dams built as lamprey barriers or incorporating lamprey barrier features in anadromous fish passage facilities, one criterion agreed upon by the 1977 Task Force on sea lamprey barriers (D. E. Reynolds, Michigan De-

TABLE 2. Sea lamprey barriers presently in use.

Lake	River	State or Province	Operational head (cm)	Other structures
Superior	Black Sturgeon	Ontario	300	
	Miners River	Michigan	46	Salmonid jumping pool
Huron	Echo River	Ontario	61–152	
	Saugeen River	Ontario	270	Fishway around dam
Michigan	Betsie River	Michigan	61	Two-pool fish ladder
Ontario	Salmon River	Ontario	91–122	

partment of Natural Resources, Lansing, Michigan, personal communication) is that a head of 45 cm should be maintained during the period of active lamprey migration. A 15- to 30-cm overhanging lip of sheet steel is placed on the top of the structure as an additional barrier to lamprey. The purpose of these design criteria is, in addition to blocking spawning-run lampreys, to (1) reduce construction costs, (2) minimize size of the backwater with resultant environmental degradation, and (3) facilitate fish passage. Design criteria suggested by engineering studies being conducted in Canada include (1) operational head of 75 cm during the summer (normal flow), (2) 45-cm head during spring runoff, (3) 15-cm head under conditions of mean annual flood, and (4) complete submergence during a 20-yr flood (T. McAuley, personal communication). A few such structures have been constructed in the State of Michigan and the Province of Ontario (Table 2). However, no in-depth studies have been undertaken to evaluate their effectiveness.

The possibility of incorporating a velocity barrier to sea lampreys in the design of some barrier dams is being considered. Field observations by Davis and Shera (1971), on migrating sea lamprey at Denny's Dam on the Saugeen River (Canada), indicated that lamprey could not move upstream past the dam when the water velocity exceeded 375 cm/s at 24.2°C. Preliminary laboratory experiments by Bergstedt et al. (1977) suggested that burst swimming speed of sea lampreys ranged from 150 to 170 cm/s at 6 or 10°C. However, the chamber used (16-cm diameter tunnel respirometer) probably restricted the swimming movements of the lamprey. Hanson (1978) tested burst swimming speeds of spawning-run lamprey in a larger, flow-through apparatus located on the lamprey weir site on the Ocqueoc River, Michigan. Water temperatures during the testing period (June 1–29, 1978) ranged from 16.5 to 25.0°C. At the highest velocity attainable with the test system, 390 cm/s, lamprey were able to swim from 1 to 3 s during any one swimming effort. Lamprey were able to maintain their position in the flume or were observed to move upstream against the current.

These observations suggest that incorporation of velocity barriers in barrier dams would be an impractical approach to preventing lamprey migration.

Future Role of Physical Barriers

Although the long-term effectiveness of barrier dams as control structures has yet to be accurately determined, such devices have and should continue to reduce the need for lampricide treatments in sea lamprey control. Physical barriers might also be used to protect habitat of native lamprey from invasion by sea lamprey and provide suitable sites for trapping adult spawning-run sea lampreys for the sterile-male-release control technique.

Besides new construction, barriers can also be made by repair work on existing dams making them lamprey-proof; making them part of highway bridge structures where road construction is planned; designing them into small-scale hydroelectric power-generating systems; or incorporating them into fish passage facilities so as to pass salmonids but deny lampreys access to spawning habitat.

APPLEGATE, V. C. 1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 55: 237 p.

APPLEGATE, V. C., AND C. L. BRYNILDSON. 1952. Downstream movement of recently transformed sea lampreys, *Petromyzon marinus*, in the Carp Lake River, Michigan. Trans. Am. Fish. Soc. 81(1951): 275–290.

APPLEGATE, V. C., AND B. R. SMITH. 1951a. Sea lamprey spawning runs in the Great Lakes, 1950. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 61: 49 p.

1951b. Movement and dispersal of a blocked spawning run of sea lampreys in the Great Lakes. Trans. N. Am. Wildl. Conf. 16: 243–252.

APPLEGATE, V. C., B. R. SMITH, A. L. MCLAIN, AND M. PATTERSON. 1952b. Sea lamprey spawning runs in the Great Lakes, 1951. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 68: 37 p.

APPLEGATE, V. C., B. R. SMITH, AND W. L. NIELSEN. 1952a. Use of electricity in the control of sea lampreys. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 92: 52 p.

BERGSTEDT, R. A., D. V. ROTTIERS, AND N. R. FOSTER. 1977. Laboratory determination of maximum swimming speed of migratory sea lampreys: a feasibility study. Res. Compl. Rep., Great Lakes Fish. Lab., Ann Arbor, MI. 4 p.

DAVIS, W. A., AND W. P. SHERA. 1971. Maximum swimming speed of spawning run sea lamprey. *In* Appendix X, p. 127. Rep. of Annual Meeting, June 1971. Great Lakes Fish. Comm., Ann Arbor, MI.

ERKKILA, L. F., B. R. SMITH, AND A. L. MCLAIN. 1956. Sea lamprey control of the Great Lakes 1953 and 1954. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 175: 27 p.

HANSON, L. H. 1978. Burst swimming speed of spawning-run sea lamprey (*Petromyzon marinus*). Res. Compl. Rep., Great Lakes Fish. Lab., Ann Arbor, MI. 11 p.

LENNON, R. E. 1970. Fishes in pest situations, p. 6–41. *In* Vertebrate pests: problems and control, Vol. 1, Chap. 2. Nat. Acad. Sci., Washington, D.C.

MCLAIN, A. L. 1957. The control of the upstream movement of fish with pulsated direct current. Trans. Am. Fish. Soc. 86: 269–284.

MCLAIN, A. L., AND W. L. NIELSEN. 1953. Directing the movement of fish with electricity. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 93: 24 p.

MCLAIN, A. L., B. R. SMITH, AND H. H. MOORE. 1965. Experimental control of sea lampreys with electricity on the south shore of Lake Superior, 1953–60. Great Lakes Fish. Comm. Tech. Rep. 10: 48 p.

SMITH, B. R. 1971. Sea lamprey in the Great Lakes of North America, p. 207–247. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1, Chap. 5. Academic Press, Inc., New York.

SMITH, B. R., J. J. TIBBLES, AND B. G. H. JOHNSON. 1974. Control of the sea lamprey (*Petromyzon marinus*) in Lake Superior, 1953–70. Great Lakes Fish. Comm. Tech. Rep. 26: 60 p.

SMITH, R. F., AND R. VAN DEN BOSCH. 1967. Integrated control, p. 295–340. *In* W. W. Kilgore and R. L. Doutt [ed.] Pest control. Part I, Chap. 9. Academic Press, Inc., New York.

STAUFFER, T. M. 1964. An experimental sea lamprey barrier. Prog. Fish-Cult. 26: 80–83.

WEBSTER, D. A., AND M. B. OTIS. 1973. Two New York facilities for fishery research and management: fish passage and collection on Cayuga Inlet and pilot artificial spawning and circulation channel at Myers Point, Cayuga Lake. Northeast Fish and Wildl. Conf., Mt. Snow, VT. June 3–6, 1973. 13 p.

WIGLEY, R. L. 1959. Life history of the sea lamprey of Cayuga Lake, New York. Fish. Bull. U.S. 59: 561–617.

U.S. DEPARTMENT OF THE INTERIOR. 1978. Draft Environmental Assessment; barrier dam program for sea lamprey control. Fish. Wildl. Serv. March 1978: 21 p.

Pheromone Communication in Sea Lampreys (*Petromyzon marinus*): Implications for Population Management[1]

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TEETER, J. 1980. Pheromone communication in sea lampreys (*Petromyzon marinus*): implications for population management. Can. J. Fish. Aquat. Sci. 37: 2123–2132.

The results of recent preference tests indicate that both male and female landlocked sea lampreys (*Petromyzon marinus*), after reaching a specific stage of sexual maturation, release pheromones which attract conspecifics of the opposite sex. In addition, sexually immature males, captured at the beginning of a spawning migration, exhibit a preference for water in which sea lamprey larvae have been held, suggesting that chemical signals, originating from populations of sea lamprey larvae in a river, may aid migrating adults in selecting a suitable spawning stream. The possible influence of a number of environmental and physiological factors on pheromone communication in sea lampreys is discussed. Synthetic pheromones have been utilized in insect pest management programs as lures for mass-trapping one or both sexes and for disrupting normal pheromone communication. Similar strategies may be applicable in an integrated program of sea lamprey population management.

Key words: pheromones, reproduction, spawning migration, sea lampreys, population management, preference behavior

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De récents tests de préférence démontrent que les grandes lamproies marines (*Petromyzon marinus*) cantonnées en eau douce, tant mâles que femelles, après avoir atteint un stade particulier de maturation sexuelle, libèrent des phéromones qui attirent les individus conspécifiques de sexe opposé. En outre, les mâles sexuellement immatures capturés au début de la migration de ponte montrent une préférence pour l'eau dans laquelle des larves de grande lamproie marine ont été maintenues. Ceci laisse penser que des signaux chimiques, émanant de populations de larves de grande lamproie marine dans une rivière, peuvent aider les adultes migrateurs à choisir un cours d'eau convenable pour la ponte. Nous examinons l'influence possible de plusieur facteurs environnementaux et physiologiques sur la communication par phéromones chez la grande lamproie marine. Dans le contrôle des insectes nuisibles, des phéromones synthétiques ont été utilisés comme appâts pour le pliégeage en masse de l'un ou des deux sexes, ou le brouillage de la communication normale par phéromones. De semblables stratégies pourraient être adoptées dans un programme intégré de gestion des populations de grandes lamproies marines.

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THE importance of chemical signals in aspects of fish behavior other than feeding is only beginning to be fully appreciated as an increasing number of studies reveal their significance, particularly in intraspecific communication. Pheromones have been implicated in a number of behavioral processes in fishes, including species recognition and schooling (Wrede 1932; Keenleyside 1955; Kühme 1963, 1964; Hemmings 1966; Miles 1968, Höglund and Åstrand 1973), parent-young recognition (Kühme 1963; Caprona 1974; Myrberg 1966, 1975; McKaye and Barlow 1976; Barnett 1977), homing (Nordeng 1971; Solomon 1973), defense (Pfeiffer 1974 for review), individual recognition (Göz 1941; Todd et al. 1967; Bardach and Todd 1970), and pair-formation and reproduction (Eggert 1931; Belding 1934; MacGinitie 1939; Seitz 1940; Tavolga 1956; Amouriq 1964, 1965; Liley 1966; Losey 1969; Gandolfi 1969; Parzefall 1970, 1973; Timms and Kleerekoper 1972; Wilkens 1972; Newcombe and Hartman 1973; Stacey and Liley 1974; Partridge et al. 1976; Thiessen and Sturdivant 1977; Crow and Liley 1979; Emanuel and Dodson 1979). Various aspects of chemical communication in fish have been reviewed by Bardach and Todd (1970), Bardach and Villars (1974), Pfeiffer (1974), Solomon (1977), and Atema (1979).

A growing appreciation of the importance of

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pheromone communication in a variety of fishes, along with the actual and anticipated success in using pheromones in population management programs for a number of insect pests (Birch et al. 1974 for review), has led to speculation about the existence of sea lamprey pheromones and their potential usefulness in a similar approach to population control.

The purpose of this paper is to summarize recent evidence for sea lamprey pheromones and to discuss the potential usefulness of such substances in an integrated program of sea lamprey control. The concept of using pheromones in pest management has evolved from work with insects and a number of parallels may be drawn which indicate not only some of the potential problems with this approach, but the most promising direction for future research as well. Several of the environmental and physiological factors which have been shown to be important in controlling the occurrence and intensity of pheromone communication in certain insects are described and speculation about their importance in pheromone communication in sea lampreys is offered.

The role of pheromone communication in the migration and reproduction of sea lampreys is only beginning to be investigated and any interpretation of the biological function of pheromones in this species will necessarily include a number of speculations, which might well prove incorrect as research progresses. The purpose of this discussion, however, is to stimulate additional experimental work in this area and point out some of the potential uses that an intimate understanding of the chemical communication system in sea lampreys may portend in terms of population management.

Evidence for Sea Lamprey Pheromones

Recent studies, in which the responses of spawning-run, landlocked sea lampreys (*Petromyzon marinus*) to substances released by sexually mature conspecifics of the same and opposite sex were observed, indicate that pheromones may play an important role in sea lamprey reproductive behavior (J. H. Teeter, J. J. Lisowski, and P. G. Bushnell, unpublished data). Sexually mature, male sea lampreys, i.e. displaying secondary sex characters, spent significantly more time in the experimental compartment of a two-choice tank, after water in which sexually mature females had been held was added (stimulus) than during the control period, when no stimulus was present (Fig. 1). Sexually mature females exhibited a similar preference for water from tanks containing sexually mature males. These preferences were not the result of a general aggregating response to the odor of other lampreys, because females showed no preference for water from tanks containing other sexually mature females, while males avoided water from tanks containing other males.

As little as 1 L of water in which a single, sexually mature male had been held for 1 h, elicited a preference response in mature females when it was added to the 78 L of water in the stimulus compartment (Fig. 2). Sexually immature females, however, exhibited no preference for water in which sexually immature males had been held, indicating that the release of the active substance(s) and/or the responsiveness of the receiving animals are correlated with sexual maturation (Fig. 2). It is unclear whether the preferences for conspecifics of the opposite sex resulted from an attraction to the stimulus, in the sense of an oriented movement toward the source, or from other behavioral mechanisms, such as decreased locomotion in the presence of the stimulus, which would also result in a preference response. For the purpose of this discussion, these preferences will be assumed to result from an attraction to the stimulus.

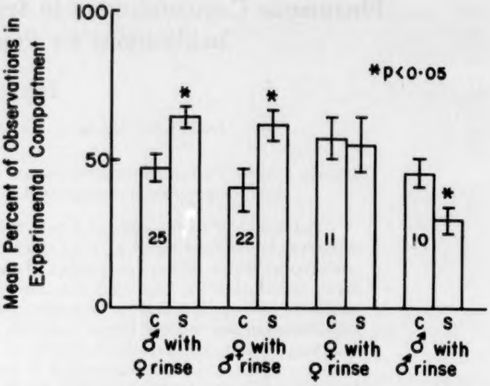

FIG. 1. Mean percent (± SE) of the number of observations of sexually mature sea lampreys, made at 5-min intervals, in the experimental compartment of an approach-avoidance trough before (C) and after (S) the introduction of water from tanks containing four to six sexually mature conspecifics of the same or opposite sex. The number of tests with each stimulus is shown in the bar for the control period. Probabilities determined using the Wilcoxon matched-pairs, signed-ranks test.

The substance(s) released by sexually mature males, which attracted females, appeared to be present in the urogenital fluid. Mucus, scraped from the skin of six sexually mature males, evoked no observable response in females, while as little as 2 mL (25.6 μL/L) of male urogenital fluid, which contained a small amount of milt, elicited a preference response (Fig. 3). Urogenital fluid, which contained no visible milt, also evoked a preference response in females, but milt alone was ineffective, suggesting that the active substance may not originate in the testes.

The substance(s) released by sexually mature females, which attracted males, appeared to be associated with ovarian fluid. Sexually mature males exhibited a preference for water rinses of eggs collected from ovulated females, but not for rinses of eggs surgically removed from unovulated females (Fig. 4).

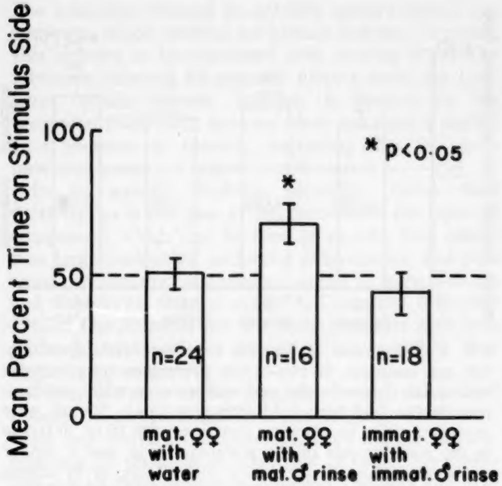

FIG. 2. Responses of sexually mature and sexually immature female spawning-run sea lampreys in two-choice preference tests between well water (control side) and either well water (blank) or 1 L of well water in which a single sexually mature or immature male had been held for 1 h (stimulus side). The 1-L samples were added to the 78 L of water in the stimulus compartment. The vertical bars represent SE, and n is the number of tests for each stimulus. Probabilities were determined using the Wilcoxon matched-pairs, signed-ranks test.

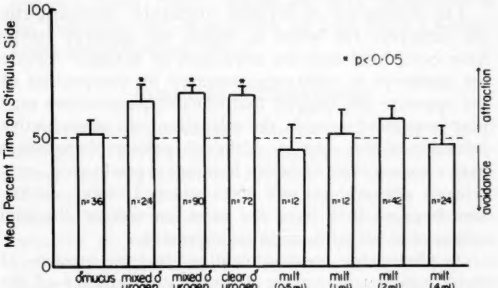

FIG. 3. Responses of sexually mature female sea lampreys in two-choice preference tests between Lake Huron water (control side) and lake water to which mucus or fractions of urogenital fluid from sexually mature males had been added (stimulus side). Mucus from the skin of six sexually mature males was used for each test. The mixed urogenital fluid contained both urine and a small amount of milt (<15% by volume). The clear urogenital fluid contained no visible milt. The milt samples contained a small, but variable, amount of urine. Samples were added to the 78 L of water in the stimulus side of the preference tank. Vertical bars represent SE, and n is the number of tests with each stimulus. Probabilities were determined using the Wilcoxon matched-pairs, signed-ranks test.

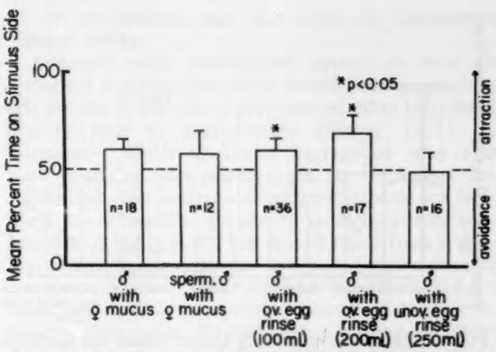

FIG. 4. Responses of sexually mature male sea lampreys in two-choice preference tests between Lake Huron water (control side) and lake water to which mucus or water rinses of eggs from ovulated or unovulated females had been added (stimulus side). Mucus from the skin of six sexually mature females or samples of the filtrate of eggs from a single ovulated or unovulated female, rinsed in 300 mL of lake water for 15 min, were used for each test. Samples were added to the 78 L of lake water in the stimulus side of the preference tank. Vertical bars represent SE, and n is the number of tests with each stimulus. Probabilities were determined using the Wilcoxon matched-pairs, signed-ranks test.

Although this suggests that release of the attractant is correlated with ovulation, preferences were also observed when males were tested with water in which sexually mature, but unovulated, females had been held. It is possible that unovulated females release the attractant, but in smaller quantities than ovulated lampreys.

Chemical signals, in addition to their potential role in the reproductive behavior of sea lampreys, may be involved in spawning stream selection by migrating adults (Moore and Schleen 1980; J. H. Teeter, J. J. Lisowski, and P. B. Johnsen, unpublished data). The number of spawning-run sea lampreys entering a river, treated the previous year with the larvacide, TFM (3-trifluoromethyl-4-nitrophenol), is frequently smaller than would be predicted on the basis of previous migrations (Moore and Schleen 1980). Although TFM, which is normally used at concentrations ranging from 0.37 to 3.7 mg/L, is avoided by spawning-run sea lampreys at concentrations greater than about 2 mg/L (Fig. 5), it is highly water soluble and is rapidly washed out of the stream after a treatment is completed (Gilderhus et al. 1975). It is unlikely that TFM is present in streams, at a concentration high enough to repel adult lampreys, several months after a treatment. Adult lampreys did not avoid water treated with 1.85 mg/L TFM and aged for two months in a tank with a sand substrate, indicating that aversive breakdown products or bacterial metabolites are not formed.

An alternative explanation of this phenomenon is

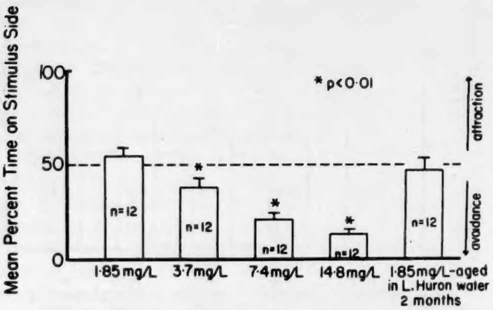

FIG. 5. Responses of sexually mature female sea lampreys in two-choice preference tests between lake water (control side) and lake water to which various concentrations of TFM (3-trifluoromethyl-4-nitrophenol) had been added (stimulus side). Vertical bars represent SE, and *n* is the number of tests with each stimulus. Probabilities were determined using the Wilcoxon matched-pairs, signed-ranks test.

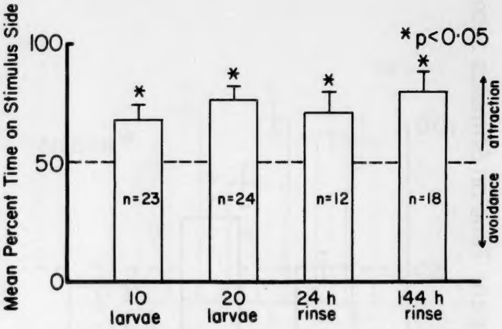

FIG. 6. Responses of sexually immature male spawning-run sea lampreys in two-choice preference tests between well water (control side) and well water in which sea lamprey larvae had been held (stimulus side). Stimuli were presented either by placing a container with 10 or 20 larvae in the stimulus side of the preference tank, and a similar container without larvae, in the control side, or by adding 4 L of water from a 38-L tank in which 36 larvae had been held for 24 or 144 h to the stimulus side, and 4 L of water from a tank without larvae, to the control side. Vertical bars represent SE, and *n* is the number of tests with each stimulus. Probabilities were determined using the Wilcoxon matched-pairs, signed-ranks test.

that upstream migrants use chemical cues emanating from the resident larval populations to aid them in finding a suitable spawning area and that removal of a significant number of the larvae by treatment with TFM reduces or abolishes these cues. This hypothesis is supported by the results of tests in which sexually immature male sea lampreys, captured at the beginning of a spawning migration, showed significant preferences for water from tanks containing sea lamprey larvae (Fig. 6). When a small plastic box containing a sand substrate and 10 sea lamprey larvae was placed in one compartment of a recirculating preference tank, and a similar box without larvae in the other compartment, sexually immature males showed a marked preference for the compartment containing the larvae. Doubling the number of larvae in the box resulted in a stronger preference (Mann-Whitney *U*-test, $P < 0.05$). Similar preferences were observed when 4 L of water from a 38-L tank, in which 36 larvae had been held for either 24 or 144 h, was used as the stimulus. The responses of sexually mature lampreys, and of sexually immature females, to water from tanks containing sea lamprey larvae have not been adequately tested. In addition, responses to water from tanks containing larvae of other species of lamprey remain to be examined.

Pheromone Communication

The term "pheromone" was introduced by Karlson and Lüscher (1959), and with the modifications proposed by Kalmus (1965), it describes a chemical or mixture of chemicals which, when released into the environment by an organism, stimulates one or more specific reactions in another individual of the same species. Two categories of pheromones have been distinguished by Wilson (1963): *releaser pheromones*, which act directly via the nervous system to stimulate an immediate and reversible change in behavior; and *primer pheromones*, which trigger relatively long lasting physiological changes, frequently involving the endocrine and reproductive systems.

The preference of sexually immature, spawning-run sea lampreys for water in which sea lamprey larvae have been held and the attraction of sexually mature sea lampreys to substances released by conspecifics of the opposite sex, suggest that releaser pheromones may play important roles in the migration and reproductive behavior of this species. Although primer pheromones may also be involved in sea lamprey reproduction, only releaser pheromones will be considered in this discussion because they have the most immediate potential application for population management.

A pheromone communication system consists of three basic components: the source or emitter of the message, the medium through which the message is transmitted, and the receiver of the message. Any attempt to manipulate the system with the goal of modifying the behavior of the receiving organism must be based upon a thorough understanding of each of these components.

In insects, pheromones are usually emitted from specialized exocrine glands, although the nature of the glands and their locations vary greatly among species (Percy and Weatherston 1974). In several species of fish, ovarian fluids from gravid females have been implicated in eliciting courtship or mating responses in males (Tavolga 1956; Amouriq 1965; Stacey and Liley 1974; Partridge et al. 1976; Crow and Liley 1979).

The substance released by sexually mature female sea lampreys, which elicits a preference response in males, also appears to be associated with ovarian fluid. The substance released by sexually mature male sea lampreys, which attracts females, is present in the urogenital fluid. Milt, however, does not elicit a preference response in females, indicating that the male pheromone may not originate in the testes.

In an aquatic medium, solubility, rather than volatility, as is the case in air, determines the types of compounds which may be used as signals. This means that large molecules, including polypeptides and proteins, can function as chemical signals in water (Gurin and Carr 1971; Carr et al. 1974; Crisp and Meadows 1963). The potential for specificity increases with both molecular size and the use of mixtures rather than single compounds.

Water is rarely static, because of wind driven and convection currents and flow due to grade. Such currents may move at velocities of many metres per second and are much more important in dispersing chemical signals than molecular diffusion (Bossert and Wilson 1963). Although chemical stimuli are nondirectional, they are generally quite persistent and may be dispersed with some directionality, over considerable distances, by water currents.

Although pheromones may be perceived by either olfactory or gustatory mechanisms, it is most likely that the responses of spawning-run sea lampreys to substances released by conspecifics are mediated by olfactory receptors. Postmetamorphic sea lampreys have a well-developed olfactory system (Kleerekoper and van Erkel 1960), which has been implicated in the detection and localization of host fishes (Kleerekoper and Mogensen 1963).

Functions of Pheromones

Pheromones are usually classified according to their biological function, e.g. aggregation, dispersion, defense, and reproduction (Wilson and Bossert 1963; Wilson 1968; Shorey 1973, 1974). On the basis of what is known about the life history and reproductive behavior of sea lampreys, several possible functions can be proposed for the responses of spawning-run lampreys to substances released by conspecifics. Three possible functions, which have implications for the use of sea lamprey pheromones in population management, are aggregation, dispersion, and release of sexual behavior.

AGGREGATION

An aggregation pheromone causes one or more conspecifics to become localized near the emitting individual. Although this type of response is commonly described as an "attraction," this term may be misleading in as much as it implies an oriented behavioral response to the source, because other behavioral mechanisms, such as decreased locomotion in the presence of the pheromone, may also result in aggregation (Shorey 1973).

Although some pheromones appear to have no biological function other than stimulating aggregation, this process is typically a precursor of other behavioral activity such as reproduction (Shorey 1977). A pheromone which stimulates aggregation may also elicit courtship and mating once the organisms are aggregated. The preferences of spawning-run sea lampreys for substances released by sexually mature conspecifics of the opposite sex do not result from a general attraction for other sea lampreys because females are not attracted by water in which other females have been held, while males avoid water from tanks containing other males. Nevertheless, a mutual attraction between the two sexes will result in an aggregation of males and females.

Although sexually immature female sea lampreys are not attracted by water in which sexually immature males have been held, it is not known if this results from the pheromone not being released by the males, from the females not responding to it, or both. If sexually immature sea lampreys are unable to detect or respond to the pheromone released by the opposite sex, then these substances probably are not important in aggregating sea lampreys prior to, or during, a spawning migration, because most of the lampreys are sexually immature at the onset of upstream movement. If, however, sexually immature spawning-run lampreys are capable of responding to sex pheromones, but are not yet releasing them, then pheromones released by a small number of sexually mature animals, present at the beginning of a spawning migration, might be used in aggregating adult lampreys pior to upstream movement or to keep them together during the migration.

The possibility that the resident population of sea lamprey larvae in a river provides an olfactory cue which aids migrating adults in finding suitable spawning areas is suggested by the attraction of sexually immature spawning-run male sea lampreys to water in which larvae had been held. An attraction of elvers of the American eel, *Anguilla rostrata*, to the odor of adults was reported by Miles (1968). In this case, adult eels may provide olfactory cues which aid the elvers in finding suitable rivers in which to feed.

DISPERSION

Pheromones that cause dispersion of conspecifics appear to have several functions including maintenance of optimal spacing for feeding and reproduction, dispersion during danger, and maintenance of territories (Shorey 1977). The release of a substance by sexually mature male sea lampreys, which is avoided by other males, may aid in dispersing the males over the available spawning habitat during nest construction. In addition, such a substance may be involved in establishing and maintaining a nesting territory. Male sea lampreys show some degree of aggression toward other males and will attempt to drive intruders from an established nest, particularly if pairing has occurred (Manion and Hanson 1980).

SEXUAL BEHAVIOR

Sex pheromones comprise a diverse group of substances, produced by either males or females, which stimulate behavioral responses in the opposite sex that lead to mating (Shorey 1977). Sex pheromones may function only in aggregating the two sexes, they may be involved in courtship and mating after other stimuli have brought the two sexes together, or the same pheromones that stimulate aggregation may also stimulate courtship and mating responses.

Pheromones, released by females at or before the time of their receptivity for mating, which cause aggregation of males, appear to be involved in the reproductive behavior of several species of fish (Amouriq 1964, 1965; Timms and Kleerekoper 1972; Newcombe and Hartman 1973; Partridge et al. 1976). In some animals, the male releases a pheromone that attracts females (Shorey 1974). In others, such as the sea lamprey, both males and females emit pheromones that stimulate aggregation of the opposite sex.

In addition to bringing the two sexes together, sex pheromones have been implicated in pair-formation in the blind goby, *Typhlogobius californiensis* (MacGinitie 1939) and several poeciliids (Amouriq 1964; Liley 1966; Parzefall 1973) and in courtship in *Bathygobius soporator* (Tavolga 1956), goldfish (Partridge et al. 1976), and poeciliids (Amouriq 1964; Parzefall 1973).

Sea lampreys are generally monogamous spawners with the pairs normally remaining together until spawning is completed (Applegate 1950). Although polygamous spawning may be common, particularly if females are numerically dominant, polyandrous nesting is rare and is usually accompanied by antagonism between the males (Applegate 1950; Manion and Hanson 1980). Pheromones released by either males or females could play an important role is establishing and maintaining spawning pairs of sea lampreys. A pheromone released by males, which usually initiate nest construction (Applegate 1950), may be involved in attracting females onto the nest prior to pair-formation. Once pairing has occurred, the mutual attraction between the two sexes might serve in maintaining the pairs.

Sex pheromones released by male insects are generally involved in courtship (Shorey 1977). Although courtship has apparently not been reported in sea lampreys, a behavior which appears to be a type of courtship has been described in river lampreys, *Lampetra fluviatilis* (Hagelin and Steffner 1958; Hagelin 1959). Females were observed circling above the males while they were engaged in nest building, often descending and passing the posterior part of their body past the head of the males. This behavior suggests the possibility of olfactory stimulation of the male by the female.

Reighard (1903) suggested that sex recognition in lampreys is a function of the female's reaction to an attachment by a male. Males, when seized by other males, released their attachment to the substrate, whereas gravid females remained attached and responded to the male with vibrating movements. Although these responses may be important in spawning, it is likely that sex recognition in sea lampreys can be accomplished solely on the basis of chemical cues.

In a number of insects, there appears to be a hierarchical arrangement of the behavioral sequence involved in the approach of a male to a female, courtship and copulation, with each successive step requiring a higher concentration of pheromone than the previous one (Bartell and Shorey 1969). A similar sequence, involving pheromone release by both sexes at certain stages, could be involved in sea lamprey spawning.

Physiological Factors Affecting Pheromone Communication

Animals do not normally produce or respond to sex pheromones at a constant level during their adult lives. Physiological mechanisms appear to control the occurrence and intensity of pheromone production, release and responsiveness to ensure that pheromone communication is functioning optimally at the appropriate time (Shorey 1974). A correlation between sexual maturity and both the amount of pheromone present and the responsiveness of the opposite sex has been demonstrated in several species of insects (Shorey et al. 1968a, b).

In river lampreys (*Lampetra fluviatilis*), sexual maturation appears to be at least partially under hypophysial control. The normal development of secondary sex characters, gonadal growth and differentiation, and spermiation and ovulation all appear to require an intact pituitary gland (Larsen and Rothwell 1972; Larsen 1980 for review). Pituitary control of sexual maturation may be expected to involve the action of gonadotropin in directly or indirectly stimulating secretion of sex steroids. Evidence that gonadal steroids are involved in stimulating the development of secondary sex characters in sea lampreys is reviewed by Hardisty (1972).

The precise relationship between the occurrence and intensity of the chemically mediated attraction of sea lampreys to conspecifics of the opposite sex and the degree of sexual maturation of the signalling and responding animals has not been determined. However, the failure of sexually immature females to respond to water in which sexually immature males have been held, indicates that pheromone release and/or the responsiveness of the receiving sex are correlated with sexual maturation. Sea lampreys enter spawning streams several weeks before the initiation of spawning activity (Applegate 1950). The relatively undeveloped state of the eggs, as well as the absence of secondary sex characters, indicate that these early migrants are less mature than the later migrants and apparently have to complete the maturation process in the spawning stream. Later migrants display more advanced stages of sexual maturity upon entry into the spawning stream and individuals reaching the nesting area during the peak of spawning activity begin nest building and spawning within a short period of time. These observations are consistent with the hypothesis that pheromone release and/or responsiveness occurs only after the antimals have reached a particular stage of sexual maturation, perhaps peaking at the time of ovulation and spermiation.

Environmental Factors Affecting Pheromone Communication

A number of environmental factors, including light intensity, temperature, air velocity and population density, are important in controlling the timing and intensity of pheromone production, release and responsiveness in several species of insects, and suboptimal levels of any one of these factors may reduce or even abolish pheromone communication (Shorey 1974).

There is general agreement that sea lamprey migration occurs during the hours of darkness, with the animals being most active from a few hours after dark until 1:30 to 2:00 AM (Lamsa 1957; McCauley 1958; Skidmore 1959). The strong negative phototaxis displayed by migrating sea lampreys appears to diminish as spawning activity begins, with nest building and spawning occurring during daylight hours (Applegate 1950). Applegate attributes the loss of the photophobic response to degeneration of the visual system. It is not known whether pheromone release or responsiveness is correlated with light intensity in sea lampreys; however, attraction to substances released by lampreys of the opposite sex has been observed both under conditions of darkness and dim illumination (J. Teeter unpublished data).

The temperatures at which insects respond to sex pheromones frequently fall within a narrow range and one would expect that in a given species, optimal release would occur in the same temperature range as optimal responsiveness in the opposite sex (Shorey 1977). Water temperature is a critical factor in determining the onset of upstream migration in landlocked sea lampreys. Migration begins when the temperature of the river rises above that of the lake (Applegate 1950; Wigley 1959). Once migration has begun, a correlation has been found between the number of animals migrating at a particular time and the temperature of the river (Applegate 1950). Upstream movement seldom occurs at water temperatures below 4.5°C and is maximum between 10 and 18.5°C. Spawning activity is also strongly influenced by water temperature. Nest building does not start until the water reaches a minimum of about 12°C and peak spawning occurs when average water temperatures reach about 18°C (Applegate 1950; Manion and Hanson 1980). Sudden drops in water temperature of as little as 1 or 2°C may result in a slowing or cessation of spawning activity (Applegate 1950). Although the effect of water temperature on pheromone communication in sea lampreys has not been systematically studied, sexually mature sea lampreys, subjected to a rapid, transient drop in water temperature of 7°C, avoided rinses of lampreys of the opposite sex, which had previously elicited an attraction (J. H. Teeter, J. J. Lisowski and P. G. Bushnell, unpublished data).

Air velocity is an important controlling factor for insect species using sex pheromones for communication, particularly over distances greater than a few cm. Velocities lower than some minimum value may result in the failure of the responding animals to localize the source of the pheromone because the pheromone is not carried sufficiently far from the source and/or because the resulting aerial trail is disrupted (Shorey 1977). High velocities and the resulting turbulent flow may make it impossible for the responding animals to orient to the source. Water velocity would be expected to have a similar effect on the distribution of waterborne pheromones.

Population density may have a profound effect on pheromone mediated behavior in a number of species of insects. Male boll weevils, *Anthonomus grandes* (Boheman), released more pheromone when they were maintained individually than when kept in groups (Hardee et al. 1969), whereas, female yellow mealworm beetles, *Tenebrio molitor* (L.), released more sex pheromone in the presence of other females than when isolated (Happ and Wheeler 1969). Whether or not population density influences the amount of attractant substances released by sexually mature sea lampreys remains to be determined.

The control of sex pheromone mediated behavior obviously is not simple. A variety of environmental and physiological factors may interact to determine the timing and intensity of pheromone communication. Which factors are important, and to what degree, will vary among species and any successful attempt to utilize sex pheromones in population management must be based upon careful experimental determination of the factors involved in regulating pheromone production, release, and responsiveness in the target species.

Use of Pheromones in Population Control

A great deal has been written about the use of pheromones for management or eradication of insect pests (Beroza and Jacobson 1963; Shorey and Gaston 1967; Jacobson 1972; Tette 1974; and others). Sex pheromones as a class possess a number of characteristics which make them attractive as control agents: (1) they are active in minute quantities; (2) they are relatively species-specific; (3) they are naturally occurring biological products and may be expected to have minimal adverse effects on nontarget species; and (4) they have a potential low cost of development (Tette 1974).

Current efforts to control insect populations by manipulating their pheromone communication systems are based upon two strategies: (1) removal of a large portion of the adults of one or both sexes by mass trapping with pheromone baited traps; and (2) disruption of the pheromone communication system so that mating does not occur (Tette 1974).

The concept of mass trapping using pheromone-baited traps is in principle simple; however, a number of difficulties have been encountered in implementing this technique (Tette 1974). The pheromone, presumably a synthetic one, must be released into the environment in such a way that it successfully competes with the natural source and yet does not disrupt communication to the point where the target sex cannot locate the trap. Traps must be designed to take into account other sensory cues which may be important in triggering the attraction to the pheromone and methods of efficiently releasing the pheromone from traps must be developed. Although some success has been attained in using mass trapping, it has proved most useful in population assessment (Birch et al. 1974 for review).

The concept of disrupting normal pheromone communication is based upon the idea that continuous release of a high concentration of the pheromone into the environment will result in: (1) the animals habituating to the pheromone; (2) the receptors adapting and thus not responding to the pheromone; or (3) the animals being unable to orient to and localize the source of the smaller amount of the pheromone released by the emitting animal (Tette 1974).

A number of potential problems may be anticipated in using the technique of disrupting pheromone communication. First, as would be the case with mass trapping, if the reproductive potential of the target species is high, as it is in the sea lamprey, it may be necessary to prevent a very large proportion of the animals from mating to have a significant effect on the population. Also, the pheromone must be stable and large amounts may be required to saturate the environment. Finally, there is the potential for effects on nontarget organisms if the pheromone is similar to that used by a closely related species (Tette 1974).

Both mass trapping and disruption of pheromone communication are potentially feasible approaches to sea lamprey population management. Sex attractants, as well as other chemical attractants, hold promise for directing migrating sea lampreys into traps or restricted areas where they could be removed, or into areas where the conditions for reproductive success are less than optimal, either in terms of the available nesting substrate or suitable areas for larvae to settle and feed. Repellents would be useful for keeping spawning stage lampreys out of the areas difficult to treat with a larvacide or out of prime spawning habitat, forcing them to use potentially less productive areas. The pheromones released by one or both sexes might be used to disrupt pair-formation or chemically mediated release of spawning behavior by continuously releasing them into the river upstream of the spawning sites.

Major advances in microanalytical and natural products chemistry in the last decade have made it possible to identify the sex pheromones for a number of major insect pests and these techniques are now being applied to the isolation and identification of sea lamprey pheromones. Identification of a pheromone, however, is not a sufficient basis for its application in population management. It must be synthesizable or available for extraction in sufficient quantities and it must be stable in the environment. In addition, the role of the pheromone in the life of the target species must be fully understood. A pheromone which functions only in courtship or which requires additional sensory cues to elicit a response is likely to be less useful than one which attracts the opposite sex over considerable distances. Finally, it has become clear from work with insect pests that disruptive approaches can intensify rather than solve a problem, or create new ones (Birch et al. 1974). This realization has led to the concept of utilizing a variety of control methods in an integrated approach designed, not to eradicate a pest species, but rather to maintain its population at an acceptable level.

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AMOURIQ, L. 1964. L'activite et le phénomène social chez *Lebistes reticulatus* (Poeciliidae: Cyprinodontiformes). Compt. Rend. 259: 2701–2702.

1965. Origine de la substance dynamogène émise par *Lebistes reticulatus* femelle (Poisson Poeciliidae: Cyprinodontiformes). Compt. Rend. 260: 2334–2335.

APPLEGATE, V. C. 1950. Natural history of the sea lamprey, *Petromyzon marinus* in Michigan. Spec. Sci. Rep. U.S. Fish Wildl. Serv. 55: 1–237.

ATEMA, J. 1979. Chemical senses, chemical signals and feeding behavior in fishes. *In* J. E. Bardach, J. J. Magnunson, R. C. May, and J. M. Reinhart [ed.] Fish behavior and its application to fisheries and management. International Center for Living Aquatic Resources Management, Manila.

BARDACH, J. E., AND J. H. TODD. 1970. Chemical communication in fish, p. 205–240. *In* J. W. Johnstone, D. G. Moulton, and A. Turk [ed.] Communication by chemical signals, Appleton-Century-Crofts, New York, NY.

BARDACH, J. E., AND T. VILLARS. 1974. The chemical senses of fishes, p. 49–104. *In* P. T. Grant and A. M. Mackie [ed.]

Chemoreception in marine organisms, Academic Press, New York, NY.

Barnett, C. 1977. Chemical recognition of the mother by the young of the cichlid fish, *Cichlasoma citrinellum*. J. Chem. Ecol. 3: 461–466.

Bartell, R. J., and H. H. Shorey. 1969. Pheromone concentration required to elicit successive steps in the mating sequence of males of the light-brown apple moth, *Epiphyas postvittana*. Ann. Entomol. Soc. Am. 62: 1206–1207.

Belding, D. L. 1934. The spawning habits of the Atlantic salmon. Trans. Am. Fish. Soc. 64: 211–218.

Beroza, M., and M. Jacobson. 1963. Chemical insect attractants. World Rev. Pest. Control 2: 1–36.

Birch, M., K. Trammel. H. H. Shorey, L. K. Gaston, D. D. Hardee, E. A. Cameron, C. J. Sanders, W. D. Bedard, D. L. Wood, W. E. Burkholder, and D. Müller-Schwartze. 1974. Programs utilizing pheromones in survey or control, p. 411–461. *In* M. Birch [ed.] Pheromones, North-Holland, Amsterdam.

Bossert, W. H., and E. D. Wilson. 1963. The analysis of olfactory communication among animals. J. Theoret. Biol. 5: 443–469.

Caprona, D. C. 1974. The effect of chemical stimuli from conspecifics on the behavior of *Haplochromis burtoni* (Cichlidae, Pices). Experientia 30: 1394–1395.

Carr, W. E. S., E. R. Hall, and S. Gurin. 1974. Chemoreception and the role of proteins: a comparative study. Comp. Biochem. Physiol. 47A: 559–566.

Crisp, D. J., and P. S. Meadows. 1963. Adsorbed layers: the stimulus to settlement in barnacles. Proc. R. Soc. Lond. B158: 364–387.

Crow, R. T., and N. R. Liley. 1979. A sexual pheromone in the guppy (*Poecilia reticulata*) (Peters). Can. J. Zool. 57: 184–188.

Eggert, B. 1931. Die Geschlechtsorgane der Gobiiformes und Blenniformes. Z. Wiss. Zool. 193: 249–558.

Emanuel, M. E., and J. J. Dodson. 1979. Modification of the rheotropic behavior of male rainbow trout (*Salmo gairdneri*) by ovarian fluid. J. Fish. Res. Board Can. 36: 63–68.

Gandolfi, G. 1969. A chemical sex attractant in the guppy, *Poecilia reticulata* Peters, (Pices, Poeciliidae). Monitore Zool. Ital. 3: 89–98.

Gilderhus, P. A., J. B. Sills, and J. L. Allen. 1975. Residues of 3-trifluromethyl-4-nitrophenol (TFM) in a stream ecosystem after treatment for control of sea lampreys. U.S. Fish. Wildl. Serv., Invest. Fish Control 66. 7 p.

Göz, H. 1941. Uber den Art und Individualgeruch bei Fischen. Z. Vergl. Physiol. 29: 1–45.

Gurin, S., and W. E. S. Carr. 1971. Chemoreception in *Nassarius obsoletus*: the role of specific stimulatory proteins. Science 174: 293–295.

Hagelin, L. O. 1959. Further aquarium observations on the spawning habits of the river lamprey (*Petromyzon fluviatilis*). Oikos 9: 221–238.

Hagelin, L. O., and N. Steffner. 1958. Notes on the spawning habits of the river lamprey (*Petromyzon fluviatilis*). Oikos 9: 221–238.

Happ, G. M., and J. Wheeler. 1969. Bioassay, preliminary purification and effect of age, crowding and mating on the release of sex pheromone by female *Tenebrio molitor*. Ann. Entomol. Soc. Am. 62: 846–851.

Hardee, D. D., W. H. Cross, E. B. Mitchell, P. M. Huddleston, H. C. Mitchell, M. E. Merkl, and T. B. Davich. 1969. Biological factors influencing responses of the female boll weevil to the male sex pheromone in field and large-cage tests. J. Econ. Entomol. 62: 161–166.

Hardisty, M. W. 1972. Gonadogenesis, sex differentiation and gametogenesis, p. 295–359. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Academic Press, New York, NY.

Hemmings, C. C. 1966. Olfaction and vision in fish schooling. J. Exp. Biol. 45: 449–464.

Höglund, L. B., and M. Åstrand. 1973. Preferences among juvenile char (*Salvelinus alpinus* L.) to intraspecific odours and water currents studied with the fluvarium technique. Inst. Freshwat. Res. Drottningholm 53: 21–30.

Jacobson, M. 1972. Insect sex pheromones. Academic Press, New York, NY. 382 p.

Kalmus, H. 1965. Possibilities and constraints of chemical telecommunication. Proc. Int. Congr. Endocrinol., 2nd, 1964 Int. Congr. Ser. 83: 188–192.

Karlson, P., and M. Lüscher. 1959. "Pheromones": a new term for a class of biologically active substances. Nature 183: 55–56.

Keenleyside, M. H. A. 1955. Some aspects of the schooling behaviour of fish. Behaviour 8: 183–248.

Kleerekoper, H., and J. A. Mogensen. 1963. Role of olfaction in the orientation of *Petromyzon marinus* I. Responses to a single amine in prey's body odour. Physiol. Zool. 36: 347–360.

Kleerekoper, H., and G. A. van Erkel. 1960. The olfactory apparatus of *Petromyzon marinus* L. Can. J. Zool. 38: 209–223.

Kühme, W. 1963. Chemische ausgelöste Brutflege and Schwarmreaktionen bei *Hemichromis bimaculatus* (Pisces). Z. Tierpsychol. 20: 688–704.

1964. Eine chemisch ausgelöeste Schwarmreaktion bein jungen Cichliden (Pisces). Naturwissenschaften 51: 120–121.

Lamsa, A. 1957. Night observations of sea lampreys at Pancake electrical barrier. Rep. Biol. Stat. Lond. Ont. 1956–57: appendix F, 28–30.

Larsen, L. O. 1980. Physiology of adult lampreys, with special regard to natural starvation, reproduction, and death after spawning. Can. J. Fish. Aquat. Sci. 37: 1762–1779.

Larsen, L. O. and B. Rothwell. 1972. Adenohypophysis, p. 1–67. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys, II. Academic Press, New York, NY.

Liley, N. R. 1966. Ethological isolating mechanisms in four sympatric species of poeciliid fishes. Behaviour Suppl. 13: 1–197.

Losey, G. A. 1969. Sexual pheromones in some fishes of the genus *Hypsoblennius* Gill. Science 163: 181–183.

MacGinitie, G. E. 1939. The natural history of the blind goby *Typhlogobius californiensis* (Steindachner). Am. Midland Naturalist. 21: 489–505.

Manion, P. J., and L. H. Hanson. 1980. Spawning behavior and fecundity of lampreys from the upper three Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1635–1640.

McCauley, R. W. 1958. The diurnal cycle of activity of spawning-run sea lamprey in the Pancake River. Rep. Biol. Stat. Lond. Ont. 1957–58: appendix F, 73–84.

McKaye, K. R., and G. W. Barlow. 1976. Chemical recognition of the young by the midas ciclid *Cichlasoma citrinellum*. Copeia (2): 276–282.

Miles, S. G. 1968. Rheotaxis of elvers of the Americal eel (*Anguilla rostrata*) in the laboratory to water from different streams in Nova Scotia. J. Fish. Res. Board Can. 25: 1591–1602.

Moore, H. H., and L. P. Schleen. 1980. Changes in spawning runs of sea lamprey (*Petromyzon marinus*) in selected streams of Lake Superior after chemical control. Can. J. Fish. Aquat. Sci. 37: 1851–1860.

Myrberg, A. A. 1966. Parental recognition of the young in cichlid fishes. Anim. Behav. 14: 565–571.

1975. The role of chemical and visual stimuli in the preferential discrimination of young by the cichlid fish *Cichlasoma nigrofasciatum* (Günther). Z. Tierpsychol. 37: 274–297.

Newcombe, C., and G. Hartman. 1973. Some chemical signals in the spawning behaviour of rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 30: 995–997.

Nordeng, H. 1971. Is the local orientation of anadromous fishes determined by pheromones? Nature 233: 411–413.

Partridge, B. L., N. R. Liley, and N. E. Stacey. 1976. The role of pheromones in the sexual behaviour of the goldfish. Anim. Behav. 24: 291–299.

Parzefall, J. 1970. Morphologische Untersuchungen an einer Höhlenform von *Mollienesia sphenops* (Pisces: Poeciliidae). Z. Morph. Tiere. 68: 323–342.

1973. Attraction and sexual cycle of poeciliids, p. 357–406. *In* J. H. Schröder [ed.] Genetics and mutagenesis of fish, Springer-Verlag, Berlin.

Percy, J. E., and J. Weatherston. 1974. Gland structure and pheromone production in insects, p. 11–34. *In* M. Birch [ed.]. Pheromones. North-Holland, Amsterdam.

Pfeiffer, W. 1974. Pheromones in fish and amphibia, p. 269–296. *In* M. Birch [ed.]. Pheromones, North-Holland, Amsterdam.

Reighard, J. 1903. An experimental study of the spawning behavior of *Lampetra wilderi*. Science 17: 529.

Seitz, A. 1940. Die Paarbildung bei einigen Cichliden. Z. Tierpsychol. 4: 40–84.

Shorey, H. H. 1973. Behavioral responses to insect pheromones. Ann. Rev. Entomol. 18: 349–380.

1974. Environmental and physiological control of insect sex pheromone behavior, p. 62–80. *In* M. Birch [ed.] Pheromones. North-Holland, Amsterdam.

1977. Pheromones, p. 137–163. *In* T. A. Sebeok [ed.]. How animals communicate. Indiana University Press, Bloomington, IN.

Shorey, H. H., and L. K. Gaston. 1967. Pheromones, p. 241–265. *In* W. W. Kilgore and R. Doutt [ed.] Pest control: biological, physical and selected chemical methods. Academic Press, New York, NY.

Shorey, H. H., S. U. McFarland, and L. K. Gaston. 1968a. Sex pheromones of noctuid moths. XIII. Changes in pheromone quantity, as related to reproductive age and mating history, in females of seven species of Noctuidae (Lepidoptera). Ann. Entomol. Soc. Am. 61: 372–376.

Shorey, H. H., K. L. Morin, and L. K. Gaston. 1968b. Sex pheromones of noctuid moths. XV. Timing of the development of pheromone-responsiveness and other indicators of reproductive age in males of eight species. Ann. Entomol. Soc. Am. 61: 857–861.

Skidmore, J. F. 1959. Biology of spawning-run sea lampreys (*Petromyzon marinus*) in the Pancake River, Ontario. M. Sc. Thesis, Univ. Western Ontario, London, Ont.

Solomon, D. J. 1973. Evidence for pheromone-influenced homing by migrating Atlantic salmon *Salmo salar* (L.) Nature 244: 231–232.

1977. A review of chemical communication in freshwater fish. J. Fish. Biol. 11: 363–376.

Stacey, N., and N. R. Liley. 1974. The regulation of spawning behavior in the female goldfish (*Carassius auratus*). Nature 247: 71–72.

Tavolga, W. N. 1956. Visual, chemical and sound stimuli in sex-discriminatory behavior of the gobiid fish, *Bathygobius soporator*. Zoologica. 41: 49–64.

Teete, J. P. 1974. Pheromones in insect population management, p. 399–410. *In* M. Birch [ed.] Pheromones. North-Holland, Amsterdam.

Thiessen, D. D., and S. K. Sturdivant. 1977. Female pheromone in the black molly fish (*Mollinenesia latipinna*): A possible metabolic correlate. J. Chem. Ecol. 3: 207–217.

Timms, A. M., and H. Kleerekoper. 1972. The locomotion responses of male *Ictalurus punctatus*, the channel catfish, to a pheromone released by the ripe female of the species. Trans. Am. Fish. Soc. 101: 302–310.

Todd, J. H., J. Atema, and J. E. Bardach. 1967. Chemical communication in social behavior of a fish, the yellow bullhead (*Ictalurus natalis*). Science 158: 672–673.

Wigley, R. L. 1959. Life history of the sea lamprey of Cayuga Lake, New York. Fish. Bull. U.S. Fish Wildl. Serv. 59: 559–617.

Wilkens, H. 1972. Über praadaptionene für das Hohlenleben, untersucht am Laiverhalten oberund unterirdischeer Population des *Astyanax mexicanus* (Pisces) Zool. Anz. 188: 1–11.

Wilson, E. O. 1963. The social biology of ants. Ann. Rev. Entomol. 8: 345–368.

1968. Chemical systems, p. 75–102. *In* T. A. Sebeok [ed.] Animal communication, techniques of study and results of research. Indiana University Press, Bloomington, IN.

Wilson, E. O., and W. H. Bossert. 1963. Chemical communication among animals. Recent Prog. Horm. Res. 19: 673–716.

Wrede, W. L. 1932. Versuche über den Artduft der Erlitzen. Z. Vergl. Physiol. 17: 510–519.

Responses of Lake Trout (*Salvelinus namaycush*) to Harvesting, Stocking, and Lamprey Reduction[1]

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Sustained yields, declines, and recovery of lake trout (*Salvelinus namaycush*) can be explained by a simple model that hypothesizes normal population regulation through density dependent body growth, coupled with depensatory lamprey mortality. The model indicates that either lamprey or fishing alone could have caused the Lake Superior decline, though they apparently operated in concert. The presence of depensatory lamprey mortality leads to a "cliff edge" in the system's dynamics, such that catastrophic changes may be repeated in the future. It is not unlikely that Lake Superior is on the verge of a second collapse. Options for dealing with potential disasters include conservative harvesting policies, development of more sensitive monitoring indicators, and modified stocking policies that may speed the coevolution of a viable lamprey/trout association.

Key words: lake trout, sea lamprey, simulation, Great Lakes, policy analysis

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Les rendements soutenus, les déclins et le rétablissement du touladi peuvent s'expliquer à l'aide d'un modèle simple fondé sur l'hypothèse que le contrôle d'une population normale peut se faire par une croissance corporelle dépendante de la densité, couplée à une mortalité anticompensatoire des lamproies. Selon ce modèle, la lamproie ou la pêche seule aurait pu causer le déclin dans le lac Supérieur, bien que le deux, semble-t-il, aient agi conjointement. La présence d'une mortalité anticompensatoire des lamproies mène au « bord de l'abime » dans la dynamique du système, de sorte que des changements catastrophiques peuvent se répéter à l'avenir. La possibilité que le lac Supérieur soit sur le point d'un nouvel affaissement ne peut être écartée. Les moyens à prendre face à d'éventuels désastres sont, entre autres, des politiques de récolte conservatrices, la mise au point d'indicateurs plus sensibles dans la surveillance et des politiques d'ensemencement différentes, capables d'accélérer la coévolution d'une association viable entre lamproies et touladis.

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THERE is a rich quantitative literature on changes in lake trout populations of the Laurentian Great Lakes. It is generally agreed that overfishing and predation by introduced sea lamprey led to catastrophic declines in the 1940s and 1950s. Extensive programs of stocking and lamprey control, coupled with reduced fishing pressure, are resulting in encouraging recoveries. There is a need now to synthesize available information into models for recovery and sustained management. There exist models for prelamprey stock dynamics in relation to fishing (Sakagawa and Pycha 1971; Silliman 1969), and for mortality rates of closed cohorts in relation to lamprey abundance (Lett et al. 1975), but these provide only fragments of the overview needed for successful policy design.

This paper develops a simulation model for longterm lake trout dynamics in relation to fishing, stocking,

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and lamprey abundance. The model attempts to explain a variety of historical observations about sustained yields, declines, and the recovery at least in Lake Superior, with a very simple hypothesis about population regulation through density-related changes in body growth rates and associated changes in age at maturity and fecundity. This hypothesis avoids the common difficulty in fish dynamics modeling of establishing a stock-recruit relationship. The model is shown to display catastrophic changes in population equilibria as harvest rates and lamprey abundance are changed. Equilibrium manifolds similar to the models of catastrophe theory are developed as "compressions" of the original simulation model, and provide a basis for discussion of future management policies.

A Model for Lake Trout Dynamics

Many factors ranging from water quality deterioration to introduced competitors have been implicated in declines of various Great Lakes fishes (Smith 1968), but for large piscivores the dominant factors appear to have been fishing and sea lamprey predation. It is difficult to separate the effects of these two, since declines in the upper lakes were associated with increased fishing effort and gear efficiency occurring simultaneously with lamprey increases (Lawrie and Rahrer 1973; Berst and Spangler 1973; Christie 1973; Wells and McLain 1973; Smith 1972). To confuse matters further, the sharpness of the declines does not imply that the critical causal agent was also changing rapidly. Ricker (1963) has noted that "big effects from small causes" are to be expected in age structured populations, i.e. a slowly changing mortality agent is quite likely to result in a large, abrupt change.

Given that lamprey predation and fishing both hit hardest at older, more fecund fish, a critical problem becomes to determine how low total egg production can be driven before recruitment is impaired. Two basic models for recruitment have been prevalent in the fisheries literature. The first ("survival response") proposes that natural mortality, growth, and fecundity of older fish are density independent processes, so that recruitment is limited through density dependent survival of juvenile fish. This hypothesis leads to the formulation of stock-recruitment curves, and the critical parameter becomes the stock size or total egg production below which juvenile survival is maximum (so recruitment becomes simply proportional to stock). The critical stock size has proven difficult to assess; a stock with this feature will crash rapidly or recover away from the break point before enough observations can be collected.

The alternative ("growth response") model for recruitment is that juvenile survival is density independent, at least for the range of juvenile densities worth considering, and that compensatory responses to increased mortality rates are generated through increased body growth rates leading to lower age at maturity and increased fecundity at age. Under this hypothesis, attention shifts from stock-recruitment to (1) the relationship between body weight (rather than age) and fecundity, and (2) rates of growth in relation to density. Given the maximum possible growth rate and a single estimate of juvenile survival, it is then simple to calculate just how high the adult mortality rate can be and still have the population sustain itself.

There are various hints in the lake trout literature that the growth response hypothesis deserves careful examination. Substantial increases in growth rate were noted during the Lake Superior and Lake Michigan declines (Sakagawa and Pycha 1971; Rahrer 1967; Wells 1980) and female age at maturity apparently dropped from 9 to 5 or 6 yr (Lawrie and Rahrer 1973; Wells 1980), while the size at maturity remained nearly constant. Unfortunately, the age at maturity observation for Lake Superior is confounded by a change in gillnet mesh sizes used for spawning stock sampling (Swanson and Swedburg 1980). Growth rates in Lake Superior after the decline may have been nearly as high as reported by Berst and Spangler (1970) in the more productive Lake Huron, suggesting a stable physiological maximum for lake trout growth in the absence of competition for resources.

It is worth noting here how large the effect can be of reduced age at maturity. Suppose the annual natural survival rate of immature fish is 80% after they reach age one, while the egg to first year survival is 1%. Then each thousand eggs laid will recruit 4.1 spawners if the age at maturity is five, and only 1.7 spawners if the age at maturity is nine. The relative effect becomes less dramatic if higher age at maturity is associated with higher survival and more opportunities for repeat spawning at larger body weights; a main motivation for developing the simulation described below was to more carefully account for such complications.

CRITERIA FOR MODEL DEVELOPMENT

We wished to develop a model that could explain at least three features of lake trout dynamics: (1) how the fish sustained relatively high and stable yields in the first part of this century (i.e. can a growth response hypothesis account for this?); (2) the catastrophic character of stock declines; and (3) lags in recovery following lamprey control and stocking. These features could not be represented by the usual equilibrium models used in fisheries population analysis.

On the other hand, the model should be as simple as possible, so that its assumptions are open to criticism and empirical test. Also, a simple model is most likely to be used by managers, who should understand it before basing decisions on it.

Models can be complicated by unnecessary detail and/or breadth of factors considered. Certainly population age and size structure is a necessary detail for a growth response model; however, the spatial structure of spawning areas, fishing, and migration might initially be ignored. To reduce the breadth of the model, the simplest approach initially is to treat mortality agents such as fishing pressure and lamprey numbers as "controlled inputs," and to hypothesize temporal stability in biological limiting factors such as food supply and water quality.

The simulation model described below appears to be the simplest that will capture the three dynamic patterns listed above (stability, decline, lags). In a subsequent section, lags in recovery will be ignored in order to produce an even simpler visual model for declines and recoveries under various stocking and lamprey control policies.

ORGANIZATION OF THE SIMULATION MODEL

The simulation was developed to predict changes in the age and size-at-age distribution of a lake trout population subject to arbitrary patterns of fishing and lamprey mortality, assuming the growth response hypothesis outlined above. By population is meant any collection of spawning stocks that are subject to similar mortality agents over time, and have similar growth, natural mortality, and fecundity responses.

The basic simulation time step is 1 yr. From the age/size distributions (1–30 yr) present at the start of each year, a spawning stock is formed and egg production and juvenile survival relationships are used to create a new age one cohort. Natural mortality and growth are then applied to the age/size distributions, and fishing mortalities are removed. Then the remaining stock is subject to lamprey mortalities to result in an age/size distribution at the end of the simulated year (start of next year). This procedure does not account for the seasonal details of growth and mortality, except to concentrate lamprey mortality in the fall just prior to trout spawning.

FECUNDITY AND JUVENILE SURVIVAL

It is assumed that the spawning population has a 50:50 sex ratio and that fecundity is related only to body weight. Eschmeyer's (1955) fecundity versus weight data was used to estimate the fecundity $e_i(t)$ of an age i female in year t as a function of her dressed body weight $w_i(t)$ in pounds (1 lb = 0.454 kg):

$$(1) \quad e_i(t) = \begin{cases} 0, & w_i(t) \leq 3.6 \text{ lb} \\ 1000 * [w_i(t) - 3.6], & w_i(t) > 3.6 \text{ lb} \end{cases}$$

(i.e. fecundity is linear in body weight above 3.6 lb, with a slope of 1000 eggs per pound). Then total egg production $E(t)$ is calculated over the numbers $N_i(t)$ by age-classes as

$$(2) \quad E(t) = 0.5 \sum_{i=1}^{30} e_i(t) N_i(t)$$

A key assumption here is that females spawn every year, at least for lower population densities.

Given total egg production, the number of 1-yr-olds the next year is calculated as

$$(3) \quad N_1(t + 1) = S_o E(t) + P(t)$$

where S_o is a combined survival rate representing egg and juvenile mortalities, and $P(t)$ is the number of yearling fish planted in year t. There are two independent estimates of S_o. First, we obtained an overall estimate for Lake Superior by running the simulation with natural mortality, growth, and fishing rate estimates reported by Sakagawa and Pycha (1971) for the prelamprey period, plus the egg production equations (1) and (2) above. S_o was then varied until the simulated population produced a steady yield of 4 million pounds. The result was $S_o = 0.008$, for a survival of eggs to maturity at age 9 of 0.14%. A simplified version of this procedure is outlined in Appendix 1, to give a minimum estimate of $S_o = 0.004$. Second, Swanson and Swedburg (1980) estimated survival to maturity directly for the Lake Superior Gull Island stock using population estimates and average fecundity. Their estimate of 0.13% is remarkably close to ours, but we used an annual survival rate from ages 1–9 of 80% while their data suggest this rate to be around 70%. They also observed a distorted sex ratio (25% females) among spawners, with the net result that they estimate $S_o = 0.04$. Luckily, it is the overall survival to maturity that is most critical for analysis of long-term population behavior.

There must exist some limits for juvenile production due to factors such as spawning habitat and food resources. In most simulations, a limit was included by calculating

$$(4) \quad N_1(t + 1) = \frac{E(t)S_o}{1 + E(t)S_o/R_m} + P(t)$$

where R_m is the maximum number of 1-yr-olds that the system can produce. For Lake Superior where N_1 was probably less than 10 million (Sakagawa and Pycha 1971), R_m was set at 25 million.

GROWTH

Table 1 shows body weights at age for Lake Superior trout prior to and during the 1950s decline, and an estimate of maximum growth, based on Berst and Spangler's (1970) Lake Huron data, needed to cause the Lake Superior age at first maturity to drop to 5–6 given a fixed weight of 3.5–4.0 lb at maturity (see eq. 1 above). Table 1 also shows simple growth times abundance estimates based on an age 1–8 annual survival rate of 0.8 and Sakagawa and Pycha's (1971) estimates of total recruitment from yield per recruit analyses (6.0 million 1-yr-olds). The sum of growth increments ($W_{i+1} - W_i$) times abundances is a crude measure of total production or resources available for growth. From Table 1 it was around 7.4 million lb/yr before the decline, and was still 7.0 million lb in 1953.

A simple density dependent growth model was con-

TABLE 1. Lake trout growth and production estimates assumed in devising the density dependent growth model. Weights in pounds. ΔW = weight gain. NΔW = Lake Superior abundance times weight gain.

	1948 Lake Superior			1953 Lake Superior			Theoretical maximum (Lake Huron)	
Age	Wt	ΔW	NΔW	Wt	ΔW	NΔW	Wt	ΔW
1	0.02	0.04	0.24	0.02	0.04	0.24	0.02	0.2
2	0.06	0.1	0.48	0.06	0.1	0.48	0.22	0.4
3	0.16	0.22	0.84	0.16	0.22	0.84	0.6	0.9
4	0.38	0.22	0.68	0.38	0.4	0.68	1.5	1.2
5	0.6	0.40	0.98	0.78	0.67	0.98	2.7	1.3
6	1.0	0.5	0.99	1.45	1.1	0.99	4.0	2.0
7	1.5	0.5	0.79	2.5	1.6	1.23	6.0	2.0
8	2.0	1.0	1.0	4.2	2.3	0.69	8.0	3.0
9	3.0	1.2	0.6	6.5	3.0	0.45	11.0	3.0
10	4.2	1.3	0.33	9.6	4.0	0.3	14.0	4.0
11	5.5	1.5	0.19	13.5	3.0	0.09	18.0	6.0
12	7.0	2.0	0.13	16.3	3.0	0.03	26.0	5.0
13	9.0	2.0	0.06	19.0	3.0	—	—	5.0
14	11.0	2.0	0.03	22.0	6.0	—	—	5.0
15	13.0	2.0	0.015	28.0	4.0	—	—	5.0
16	15.0	2.0	0.007	—	—	—	—	5.0
17+	17–43	2.0	—	—	—	—	—	5.0

structed by assuming that a fixed total resource *R* (8 million lb for Lake Superior) is shared across age-classes, with each age acquiring an annual share proportional to its average body weight at the start of the year. The increment r_i in body weight for age *i* animals is calculated as

$$(5)\quad r_i(t) = \frac{w_i(t)}{\sum_i w_i(t)N_i(t)} R$$

and is constrained to be at or below $r_{\max i}$ (maximum growth increment) as given in the "maximum growth" column of Table 1. Equation (4) simply says that growth is proportional to body weight and total resources, and inversely proportional to total biomass of competing fish ($\Sigma w_i N_i$). Simulated body weights are incremented as

$$(6)\quad w_{i+1}(t+1) = w_i(t) + r_i(t)$$

The growth model (eq. 5) has at least two serious weaknesses that could not be corrected without seriously complicating the analysis. First, fish of different sizes have different resources available to them, so abundance of older fish for example does not necessarily imply slower growth in young fish as equation (5) would suggest. It is a conservative assumption to place all fish in direct competition with one another (for example, simulated stocking policies may then result in delayed maturity of natural fish). Second, there may be dynamic interactions between trout and their forage populations; Smith (1972) has expressed concern about the stability of stocks of introduced forage fishes (smelt, alewife) relative to the natural complex of forage species. *R* may in fact be a highly variable and unpredictable quantity in the future.

NATURAL AND FISHING MORTALITY

Sakagawa and Pycha (1971) review estimates of lake trout natural mortality, and suggest it to be around 20% per year in the absence of lamprey predation. Slightly higher estimates were obtained by J. H. Kutkuhn (U.S. Fish and Wildlife Service, Ann Arbor, MI, personal communication) and Pycha (1980) for Lake Superior in recent years. There is no evidence that natural mortality rates are reduced when densities are low; for example Budd et al. (1969) found similar age 1–3 survivals for several cohorts of trout planted in Lake Huron after the main collapse. In the simulation, a natural mortality of 20% is removed from each age-class each year before the fish are subject to fishing and lamprey mortality.

Fishing mortality rates were reported for Lake Superior by Sakagawa and Pycha (1971), and more recently by Pycha (1980). They estimated the pre-lamprey (sustained) removal rate at about 40–50% for ages 10 and higher. The simulation assumes 50% exploitation rates on fully vulnerable ages when the input fishing effort is equal to 1.0 (i.e. 100% of pre-1940 average for Lake Superior, following Lawrie and Rahrer 1973). For varying effort levels and ages of fish, harvest rates are calculated as

$$(7)\quad h_i(t) = 1 - e^{-qv_i(t)E(t)}$$

where $h_i(t)$ is the proportion of age *i* fish harvested in year *t*, $q = 0.69 =$ catchability coefficient, $E(t) =$

effort in year t, and $v_i(t)$ is a size dependent relative vulnerability estimated from body weight $w_i(t)$ of age i animals. $V_i(t)$ is assumed equal to zero for $w_i(t) <$ 1.5 lb, and increases linearly to 1.0 for $w_i(t) = 4.0$ lb. This selection pattern can be altered to reflect new fishing regulations; as is, it makes the fish fully vulnerable to exploitation shortly after they reach maturity.

Annual harvest in pounds is calculated in the obvious way, as

$$H(t) = \sum_{i=1}^{30} h_i(t)\, N_i^*(t)\, w_i(t) \tag{8}$$

where $N_i^*(t)$ is age i abundance after the 20% natural mortality is removed. It is usual in fisheries models to integrate mortality rates and growth in terms of a yield equation where all processes are assumed to occur simultaneously. For this study it was felt that the increased precision of such estimates is hardly justified in view of the available data.

A key future problem in the Great Lakes may be the developing sportfishery. Harvest rates in the model should be interpreted as totals across commercial and recreational users.

LAMPREY MORTALITY

It is assumed that the total feeding population of lampreys $L(t)$ is fixed in any year by control actions or biological factors independent of lake trout abundance (i.e. no obligate predator–prey coupling). The problem then becomes to estimate the number of attacks per lamprey as a function of trout abundance (the functional response to prey density of Holling 1959) and trout mortality in relation to the number and timing of attacks. The following discussion is based on the quantitative summaries of lamprey biology prepared by Farmer (1980) and by Lett et al. (1975).

If lamprey distribute their time between attacking and searching for prey, and do not develop search images or other behavioral tactics for switching to abundant prey types, then the number of attacks they make in any short time period can be assessed with the "multispecies disc equation" (Charnov 1973; Murdoch 1973) as

$$NA_i = L(t) a_i p_i N_i(t) / (1 + \sum_j a_j p_j t_j N_j(t)) \tag{9}$$

where NA_i is the number of attacks on type i (i.e. age-class i) prey in the short period, $N_i(t)$ is abundance of that prey type, a_i is the "rate of effective search" (Holling 1959) for prey type i, p_i is probability of attachment to type i given that a lamprey has encountered it, and t_i is the amount of time spent attached and subsequently not searching for each attack on type i prey. The denominator term of equation (9) says that attacks on any type i will be diluted as abundance of other prey types increases, especially if those other types have higher a_j, p_j, or t_j. The complex simulation of Lett et al. (1975) can be reduced essentially to equation (9) with a_i very large (i.e. lamprey are very efficient searchers).

For all the research that has been done on sea lamprey in the Great Lakes, two key components of the attack functional response have never been measured: $L(t)$ and a_i. There is a similar lack of information on the probability of death *per attack* as a function of fish size. Minimum estimates $L(t)$ can be obtained from barrier/weir catches (Lawrie 1970), and Smith (1971) has extrapolated index barrier catches to totals for Lake Superior.

If lamprey are efficient searchers, and if they do not actively switch (a_i dependent on N_i) to other prey types when lake trout are scarce, then they will exert a depensatory mortality effect with profound policy consequences. Two lines of evidence suggest that this is indeed the case. First, mortality rates of lake trout were very high after the declines, and remained high for some time after lamprey control began. Second, there appeared to be a threshold stocking rate below which no yearlings could survive to marketable sizes in Lake Superior, and this threshold became smaller as stocked fish accumulated in the system (Lawrie and McCallum 1980).

Since the a_i appear to be large, it is reasonable to replace the functional response equation (9) with a simpler depensatory mortality model that compresses the results of Lett et al. (1975) as

$$C_i = \frac{l_i N_i(t) C_o L(t)}{\sum_i l_i N_i(t) + B_o} \tag{10}$$

$$C_i \leq N_i(t) w_i(t)$$

where C_i is the total biomass of prey type i killed in a year, l_i is the relative vulnerability or "attractiveness" of prey type i, C_o is the total pounds of prey killed per lamprey, and B_o is an effective biomass of prey other than lake trout available to lampreys. For this study, it was assumed that $l_i = w_i(t)$ for $w_i(t) \geq 1.0$ lb, and $l_i = 0$ for $w_i(t) \leq 1.0$ lb (i.e. lamprey concentrate their atttacks on larger fish when these are available). C_o was taken to be 45 lb. For most simulations, the conservative assumption that $B_o = 5.0$ million lb was chosen. Equation (10) simply says that lamprey will kill $C_oL(t)$ pounds of fish in year t, and this will be apportioned across the total available fish biomasses with preference given to larger and more abundant age-classes. If $C_oL(t)$ is more than the total available biomass, then all the fish are killed. Equation (10) will generally tend to overestimate mortalities at low trout stock sizes; this is a conservative error in relation to assessment of stocking levels needed to overcome lamprey impacts.

Model Predictions in Relation to Historical Patterns

Pycha and King (1975) and R. L. Pycha (personal communication in Heinrich et al. 1980) have estimated

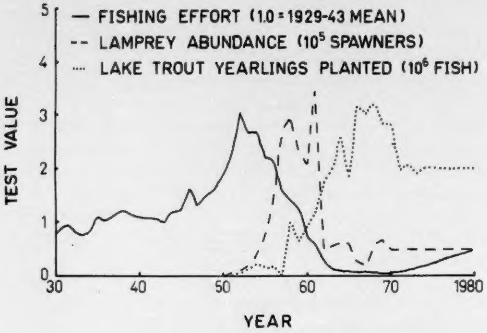

FIG. 1. Lake Superior test inputs for evaluation of Lake trout simulation. Data from Pycha and King (1975), Smith (1971), Heinrich et al. (1980), and R. L. Pycha (personal communication).

fishing effort, stocking, harvest, and abundance of Lake Superior trout for 1929–78. Their estimates of Michigan waters fishing effort, reported total stocking, and Smith's (1971) estimates of lamprey abundance were used to "drive" a test simulation (Fig. 1). The initial (1930) age and size distributions for this simulation were chosen to agree roughly with Sakagawa and Pycha's (1971) equilibrium yield assessments.

Simulated trends in abundance and harvest agree quite well with the data (Fig. 2) except that the model produces a sharp peak in harvest just before the 1952–60 decline, and the decline is faster than was observed. Indeed, the simulated harvests would better fit the Lake Michigan pattern as reported by Wells and McLain (1973). The simulated recovery from 1960 to 1970 is somewhat more dramatic than was actually observed in Lake Superior, probably because planted fish in the simulation were assumed to mix completely with natural fish and to have the same reproductive success. In agreement with Pycha's abundance data for the 1970–78 period, the model predicts a leveling off or decline in abundance after 1970. It should be noted that the model versus observed abundance comparisons are not precise; the model output represents total abundance by sharply defined size-classes, while the observed abundance index (by gill net sampling) represents a smearing and smoothing across size and age-classes.

The model predicts a very sharp increase in abundance of 4.0 lb and larger fish around 1968–72 for Lake Superior (Fig. 2). This agrees with the observed appearance of larger fish (11+ ages) in the Gull Islands shoals spawning stock (Swanson and Swedburg 1980), in Michigan waters catches (Pycha 1977), and with recent estimates of survival rates in Minnesota waters (Anon. 1977).

As indicated by the simulated proportion of native yearlings (Fig. 3), the model predicts little contribution by natural spawners until about 1975–80 (when yearlings produced in 1969–72 are fully mature). No assumption was made in this case about stocked fish being less successful spawners, as Wells (1980) has reported for Lake Michigan, so Fig. 3 doubtless is an overly optimistic assessment of production trends. However, Lawrie and McCallum (1980) report that a rapid increase in native fish is now occurring in Lake Superior.

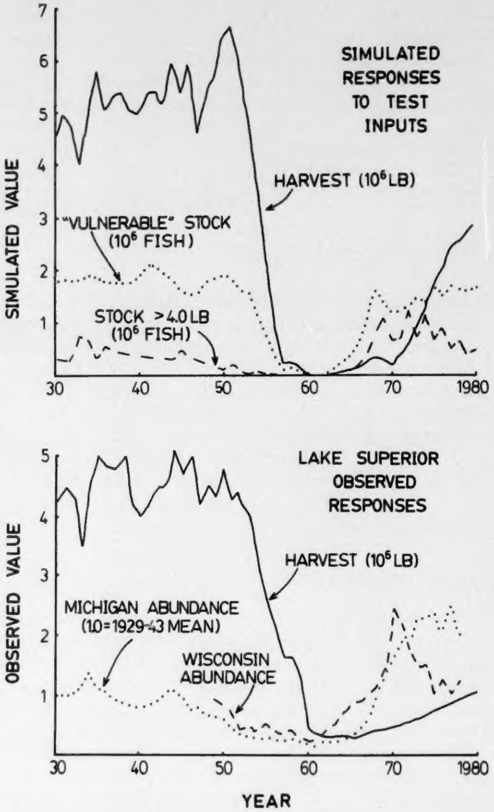

FIG. 2. Simulated harvest and population abundance measures resulting from the test inputs of Fig. 1, compared to historical data. "Pop > 4.0 lb" means total number of fish with dressed body weights greater than 4.0 lb. See text for explanation of "vulnerable pop."

Additional details of the Lake Superior baseline simulation are presented in Fig. 3. The simulated age at maturity drops after 1950, but then increases sharply again in the 1970s. The increase is due to slower growth associated with the recovery in abundance. Evidence of slower growth and later maturity in the 1970s has not been reported in the literature, though R. L. Pycha (U.S. Fish and Wildlife Service, Ashland, WI, personal

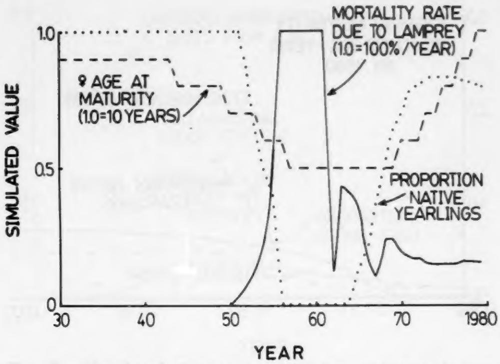

FIG. 3. Simulated changes in native fish contribution, age at maturity, and lamprey mortality on 4+ lb fish, for Fig. 1 test inputs.

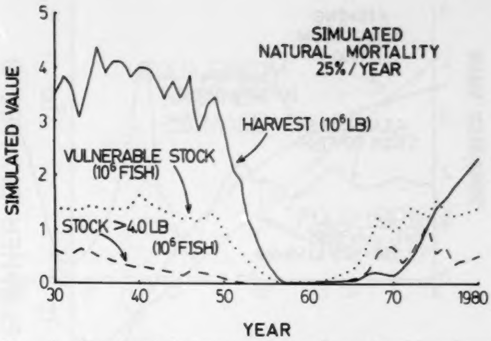

FIG. 4. Simulated harvest and abundance resulting from assumption that natural mortality rate is 25% rather than 20%. All other parameters and inputs as in Fig. 2.

communication) agrees that growth rates dropped between 1970 and 1975. Swanson and Swedburg (1980) report relatively fewer age 6–7 spawners after 1966.

The simulated lamprey mortality rate on older (>4.0 lb) fish rises to 100% after the decline has been initiated by overfishing, but then drops very quickly in the mid-1960s. The drop is not due simply to lamprey control; simulated lamprey abundance is reduced sharply in 1962 (Smith 1971). Both components of the predator:prey ratio are changing, as the first large cohorts of stocked trout attain sizes where they are vulnerable to lamprey. J. H. Kutkuhn (personal communication) estimated the lamprey mortality rate on 5–8-yr-old trout in southern Lake Superior to drop from 54% in 1965 to 20% in 1967, then to rise slightly in 1968–69. Lawrie and McCallum (1980) report a sharp drop in mortality for the 1965–70 period, evidenced by the relative number of planted fish reaching "marketable" size. Pycha (1980) reports a sharp drop in mortality rate, but between 1968 and 1974, for Michigan waters of the lake. However, higher estimates (53%) of recent lamprey mortality on older fish were reported for Gull Island shoals by Swanson and Swedburg (1980).

R. L. Pycha (personal communication) suggested that the Lake Superior natural mortality rate may be closer to 25–30% than the 20% originally assumed, and that this could explain why the model erroneously produced a peak in yield just before the collapse. Figure 4 shows results of a test simulation with natural mortality set at 25% (other parameters and inputs as in Fig. 1 and 2). Pycha's second suggestion is obviously confirmed. An interesting but not practically testable hypothesis from Fig. 2 and 4 is that differences in patterns of decline between the Great Lakes were due to historical differences in natural mortality rates.

Three simulations intended to assess the relative impacts of fishing versus lamprey mortality are shown in Fig. 5. In case 1, fishing was sharply curtailed in 1950 (to 10% of 1929–40 average), while the historical lamprey and stocking patterns were maintained. In this case, the lampreys were still able to devastate the stock, though it recovered after lamprey control. In case 2, fishing and stocking were maintained while the lamprey was eliminated completely. Fishing was still able to cause a crash, but stocking made the recovery quite rapid. In case 3, the historical lamprey and effort patterns were maintained, but the stocking program was eliminated. In this dramatic case, there is no recovery since there is no way to overcome the depensatory influence of lamprey mortality.

The test simulations in Fig. 5 show that the model does not single out one causal agent to explain all the changes in Lake Superior. Changes in fishing, lamprey, and stocking are all needed to make the growth response population model agree with historical patterns. A subsequent section will attempt to develop simplified representations of the interplay among factors.

Is Another Catastrophe Coming?

During SLIS, A. Wright (Michigan Dep. Natural Resources, Lansing, MI 48909, personal communication) suggested that we explore the effects of differentially low reproductive success by planted fish, coupled with uncertainties about exploitation rates due to sports and native Indian fisheries. Figure 6 shows results from two scenarios in which it was assumed that planted fish have only 10% the effective fecundity (at all ages) of native fish. The first scenario roughly assumes Pycha's (1980) estimate of recent total exploitation rate, and the model predicts a satisfactory pattern of long-term recovery. The second scenario assumes an exploitation rate that would be difficult to separate statistically from Pycha's, yet it predicts a collapse in native stocks after 1980. While substantial long-term yields are maintained in both scenarios, there is an obvious decrease due to the loss of natural production in the second one.

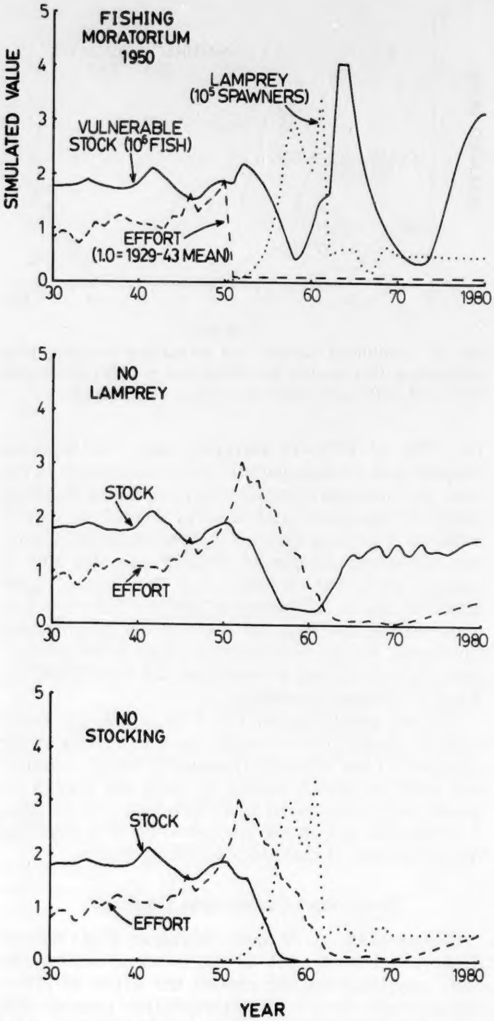

FIG. 5. Test simulations showing effects of variation from the historical pattern of inputs.

There is no way with available data to establish which of the two scenarios in Fig. 6 is more accurate. The reproductive success of planted fish is difficult to measure, especially considering that early plantings were often in areas unsuitable for spawning and there was at least some tendency for fish to home back to these areas. Likewise, estimates of fishing mortality rates (by tagging studies and catch curves) are notoriously unreliable. Even if reproductive and harvest parameters were known exactly, there are other major uncertainties such as the natural mortality rate.

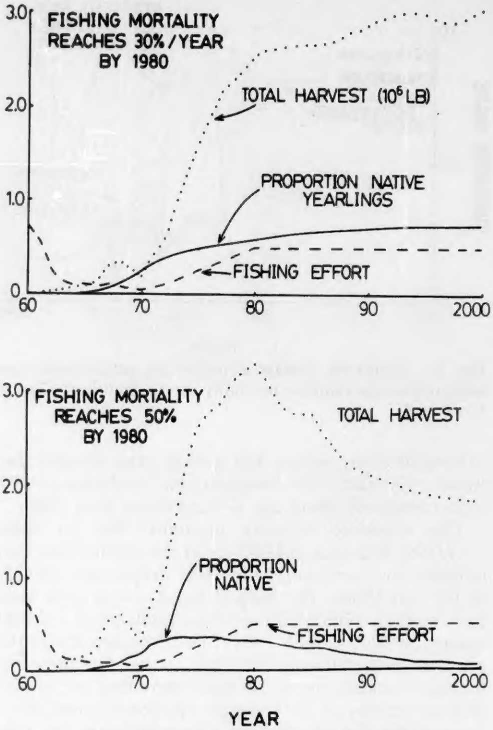

FIG. 6. Alternative predictions for Lake Superior, assuming stocked fish have only 10% the reproductive success of native fish.

Lake Superior may be poised at the brink of another disaster in terms of native lake trout production, and only experience will tell for sure. Other SLIS authors express these concerns (Lawrie and McCallum 1980; Pycha 1980). It would therefore seem prudent to seek monitoring indicators that give the earliest possible warning of collapse. Figure 7 shows four indicators suggested by scientists at SLIS, for the native collapse scenario of Fig. 6. The first warnings of trouble are decreases in the native yearling ratio and in the abundance of large fish. The vulnerable stock size does not decline for 10–15 yr, at least partly due to increased growth rates that place fish into vulnerable size-classes before they have been subject to as much natural mortality. Substantial increases in body weight of young fish (age <8 yr) presage the collapse by a few years.

As a sensitive and relatively inexpensive warning measurement, the proportion of native yearlings emerges as a key monitoring priority. Indeed, it might be worthwhile to stabilize stocking rates and locations over the next decade or two, just to avoid confounding

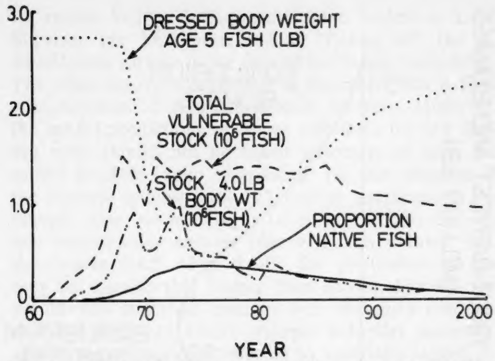

Fig. 7. Simulated changes in possible monitoring indicators for the second scenario (native fish collapse) in Fig. 6.

the measurement. This would imply foregoing stocking programs aimed at producing "put-and-take" fisheries, and experimental stocking to increase spatial and genetic diversity of spawning.

Compression for Policy Analysis

In several resource case studies, we have found it useful to "compress" the system simulation into much simpler graphical or topological models that capture key qualitative behaviors (i.e. declines and recoveries) in terms of a few control and performance variables (Clark et al. 1979; Holling 1978; Holling et al. 1979). The simplest example of such a compression in fisheries would be to plot equilibrium yield as a function of fishing effort. Generally, the idea is to look at how equilibria of "fast" or response variables relate to changes in "slow" or control variables. The equilibrium manifolds of catastrophe theory (for ecological examples, see Jones 1975; Jones and Walters 1976) result when the equilibria show large, discontinuous changes with small changes in the control variables. Given the equilibrium representation, the system can be approximately "simulated" by tracing the movements of the fast variable equilibria as the control variables are manipulated.

It is possible to develop equilibrium pictures of lake trout biomass (or other population measures) in relation to the control variables effort, lamprey abundance, and stocking, simply by running the simulation many times with different inputs and starting conditions. However, many of the results to be obtained this way can be understood with a much simpler, graphical starting point. Figure 8 shows roughly how equilibrium recruitment and spawner biomass vary in relation to one another, for a fixed lamprey abundance and fishing mortality rate. The population can be at equilibrium only when the two curves cross (both recruitment and spawning stock must be at equilibrium). The equilibrium curve for recruits *R* as a function of spawner

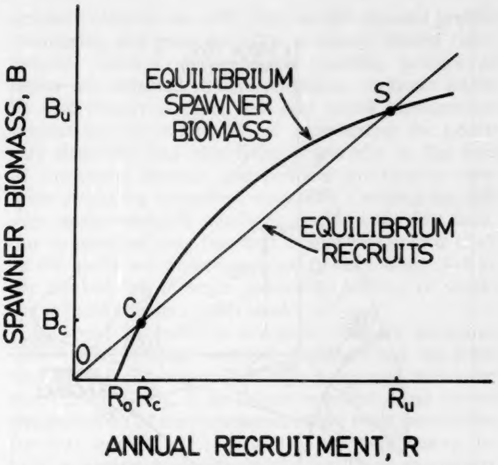

Fig. 8. Equilibrium recruitment and spawner biomass in relation to one another, for an intermediate lamprey stock and fishing rate. Explanation in text.

biomass, *B*, arises very simply: with fixed juvenile survival, recruitment is just proportional to egg production which is almost proportional to spawner biomass. The reciprocal relationship, *B* as a function of *R*, is a bit trickier to see: for recruits *R* less than a critical value R_o, the spawning biomass will be effectively zero due to depensatory mortality by lamprey. Given higher recruits (i.e. through supplemental stocking), the spawning biomass will rise to some upper limit set by resources available for growth and by fishing mortality. Lawrie and McCallum (1980) provide direct evidence for the existence of R_o; their marketable abundance represents potential spawning stock. Their relationship would be curved as in Fig. 8 if they had plotted abundance as biomass and if growth rates have decreased as suggested by R. L. Pycha (personal communication).

Points *S* and *O* in Fig. 8 represent locally stable equilibria; the stock will tend to return to these points if not disturbed too much. On the other hand, *C* is a "critical point"; if spawning biomass is pushed below B_c, it will tend to produce a recruitment too small to replace itself, and the stock will drop toward 0. Above B_c, the stock will tend to produce more recruits than needed to maintain itself, and the system will move toward *S*.

Both of the curves in Fig. 8 will move if fishing or lamprey abundance are altered. Increasing lamprey abundance causes the *B* curve to move down and to the right, and the *R* curve to steepen. Increased fishing has essentially the same effect. The result is to move the equilibria *S* and *C*: the upper equilibrium biomass B_u moves downward, and the critical B_c moves upward to meet it. If we consider the difference $B_u - B_c$ as a

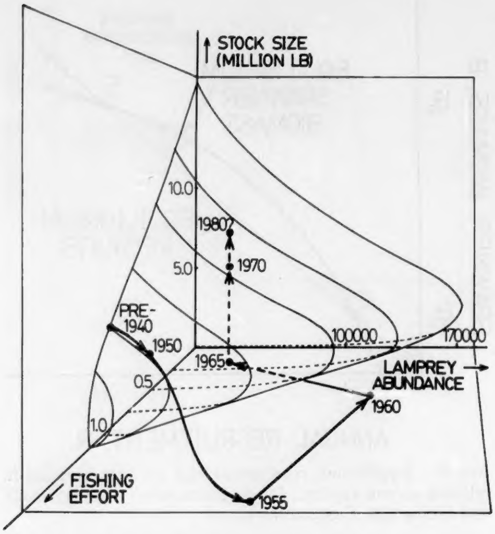

FIG. 9. Equilibrium stock sizes as a function of fishing effort and lamprey population. Upper curved surface represents locally stable equilibrium points; folded undersurface represents unstable equilibria where stock might crash to zero or rise to upper surface. Lake Superior history shown as "falling off the manifold" between 1950 and 1955.

measure of the "domain of stability" of B_u, then fishing and lamprey cause this domain to be smaller. Also, higher B_c implies that higher stock rates (effective R) are needed to overcome the lamprey effect. At high enough fishing and/or lamprey mortality rates, B_c and B_u coincide or disappear entirely; if the system is initially near B_u, the result is a catastrophic crash toward the remaining stable point 0.

The equilibria B_c and B_u can be plotted as a function of fishing rate and lamprey abundance; the result is a folded surface as shown in Fig. 9. A cross-section through this "equilibrium manifold" is shown in Fig. 10. Points for Fig. 9 and 10 were estimated with the simulation model, after the graphical analysis presented above had helped to define key variables and ranges of control values worth testing. Points for B_u (upper fold of equilibrium surface) were computed by running the simulation to equilibrium while holding the respective fishing effort and lamprey abundance constant, starting with a high (1930) initial stock size. The folded undersurface in Fig. 9 represents values of B_c; these were estimated by running the simulation with the population initially zero and with increasing stocking rates, until stocking resulted in a value of B that could just replace itself.

Simulated stocking rates needed to achieve spawning biomass B greater than the critical B_c, starting from a decimated state, are shown in Fig. 11. Note that for fishing rates much above the prelamprey average, or for lamprey stock size much above 100 000, there is no stocking rate that would permit recovery.

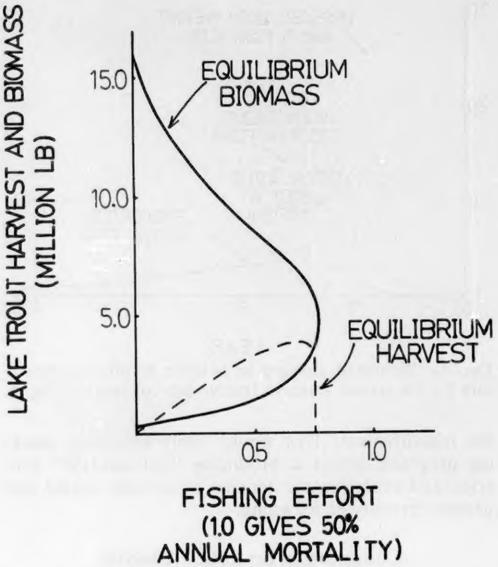

FIG. 10. Simulated equilibrium trout biomass (millions of lb, 1+ yr old fish) and harvest for Lake Superior, for a fixed lamprey stock of 50 000, as a function of fishing effort. The biomass curve is a cross section through the curved surface in Fig. 9.

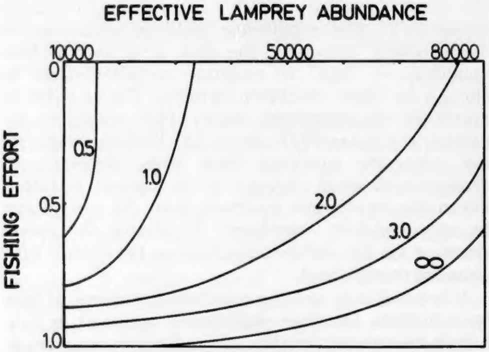

FIG. 11. Simulated isocontours of annual stocking rates (millions of yearlings) needed to reestablish lake trout in Lake Superior after a crash, for different fixed levels of fishing effort (1.0 = 1925–40 average) and lamprey abundance.

Figures 9, 10, and 11 provide useful qualitative compression of key behaviors of the simulation model.

As shown in Fig. 9, the catastrophic decline in Lake Superior can be represented as "falling off" the B_u equilibrium surface in the face of increasing mortalities. The rapid recovery beginning in the mid-1960s is likewise represented as a catastrophic increase. However, the model predictions of upper equilibria for low fishing rates should not be taken seriously; in fact, the model predicts cyclic recruitment for this situation if the juvenile habitat limit (25 million yearlings) is removed. Also, no account is taken of the differentially low reproductive success observed with planted fish; the "lower fold" (Fig. 9–10) for population escape may be considerably higher than shown. Finally, the equilibrium manifold pictures will obviously not predict short-term (<10 yr) changes with any accuracy, since these changes are affected by transient, lagged responses in population age and size structure.

Policy Implications

The model outlined above makes several suggestions about lake trout recovery and about longer term, sustained management. In the following discussion, it will be assumed that (1) there will be some control in the future over the fisheries, particularly the developing sportfisheries; (2) stocking will be conducted so as to produce mature fish that return to useable spawning areas (i.e. stocked fish as successful as mature fish); and (3) there will exist lamprey control methods that can generally maintain (not allowing increases) existing lamprey abundance.

An obvious implication of the previous section is that lamprey create "recovery thresholds" for stocking programs. A modest stocking program will go entirely to waste, at least in terms of reestablishing natural spawning, rather than simply prolong system recovery. While recoveries in Lakes Superior and Michigan might have been initiated by somewhat lower stocking rates (Fig. 11), it appears that the choice of 2–3 million fish/yr was wise especially in view of uncertainties about effective lamprey abundance.

MANAGEMENT ON THE CLIFF EDGE

A more serious problem is suggested by Fig. 9–10, and the scenarios shown in Fig. 6. It appears that sustained management will become a matter of operating relative to a catastrophic cliff, where the location of the cliff edge cannot be ascertained precisely and is likely to move anyway due to uncontrollable changes in apparent lamprey abundance (i.e. appearance of shoal spawning stocks, changes in abundance of alternate prey), fishing technology, and resources available for trout growth. With current sea lamprey stocks of perhaps 40 000–60 000 spawners in Lake Superior, it should eventually be possible to maintain sustained yields around 3.0–3.5 million lb, or three-quarters of the historical average (Fig. 10).

But to operate near maximum sustained yield, dangerously close to the cliff edge, would demand precise monitoring and great flexibility to change fishing rates, lamprey control, and perhaps stocking policies as errors are detected. Such continuing vigilance might be theoretically possible, but real world management institutions are not noted for maintaining the necessary flexibility and objectivity (especially in the face of short-term success and political pressure to continue producing immediate rewards). Crossing the cliff edge again would be nearly as costly as the first time, due to response time lags that cannot be avoided (3–5 yr for increased lamprey control to take effect, 5–8 yr for stocked fish to begin spawning, 5–10 yr of stocking to build effective buffer stock).

It would be futile to invest in research programs aimed at eliminating uncertainties regarding the location of the cliff edge. The edge is crossed when the two curves in Fig. 8 no longer intersect; these curves depend on *all* of the parameters of the trout (fecundity, survival, growth, etc.) as well as the quantitative details of lamprey mortality and fishing. These parameters are mutable and subject to uncontrolled environmental changes, so just to measure them once would not be sufficient.

Fortunately, there are indicators that can be monitored as early warning signals of impending decline (Fig. 2 and 7). The relative abundance of older (11+ yr) fish drops steadily as the cliff edge is approached (Fig. 2), as does the survival rate of ages 8+ fish. Growth rates increase steadily, and the proportion of native fish may drop sharply. Less sensitive indicators are the lamprey wounding/scarring rates, though these appear to be highly popular measures among Great Lakes researchers and managers; by the time they provide a really clear signal of increased mortality, the decline may already be far along. About the worst possible indicator is total harvest.

Successful management near the cliff edge would demand the careful development of feedback control policies for choosing harvest and lamprey control rates as a function of monitoring indicators. The required analysis is beyond the scope of this study; possible approaches are reviewed in Walters and Hilborn (1978).

ALTERNATIVE APPROACHES

There are at least two alternatives to management on the cliff edge. First, management may simply stay well away from dangerous situations, by adopting very conservative harvesting rates coupled with continued intensive lamprey control. The idea would be to maintain stock sizes large enough to absorb unexpected changes. Unfortunately, it is difficult to decide just how conservative to be. Figure 10 suggests that yields of 1–2 million lb/year could be taken "very safely" from Lake Superior, but many resource users would doubtless be willing to risk a 3.0 million lb/year rate. Statistical decision theory is of little help in this case, since any assignment of probabilities to different assessments of the cliff edge location would be purely arbitrary.

The second alternative is to redesign the basic topology of the system, so as to eliminate the cliff edge entirely. This has essentially been the objective in Lake Huron, where it was hoped that stocking of splake would result in rapid growth and early maturity, so that each cohort could reproduce itself before being decimated by lamprey and fishing (Berst and Spangler 1970). Since the cliff edge arises through the depensatory effects of lamprey predation, the problem is to speed the development of a coevolved predator/prey association where the prey are not decimated regularly by the predator. Moav et al. (1978) consider this a general problem in fisheries, and suggest policies similar to the Lake Huron experience. Their optimism has not yet been supported by events in the Great Lakes, but it is probably still too early to reject the approach.

Probably the best option now is to manage very conservatively (low harvests, continued lamprey control), while aiming stocking programs more deliberately at discovering and injecting lamprey resistant genotypes into the system. Nature discovers viable combinations by massive, trial and error experiments that mostly are dismal failures. Man can speed up this process considerably, provided there is willingness to accept and profit from the failures.

Anon. 1977. Lake Superior commercial fish assessment studies status of Lake Superior stocks — 1976. Minnesota Dep. Nat. Res. Fish Wildlife Div., Sect. Fish. Published as Appendix V, 1977 Minutes of Lake Superior Committee, Great Lakes Fishery Commission, Ann Arbor, MI, p. 43–64.

Berst, A. H., and G. R. Spangler. 1970. Population dynamics of F1 splake (*Salvelinus fontinalis* × *S. namaycush*) in Lake Huron. J. Fish. Res. Board Can. 27: 1017–1032.

1973. Lake Huron: the ecology of the fish community and man's effects on it. Great Lakes Fish. Comm. Tech. Rep. 21: 41 p.

Budd, J. C., F. E. J. Fry, and P. S. M. Pearlstone. 1969. Final observations on the survival of planted lake trout in South Bay, Lake Huron. J. Fish. Res. Board Can. 26: 2413–2424.

Charnov, E. L. 1973. Optimal foraging: some theoretical explorations. Ph.D. dissertation, Univ. Washington, Seattle, WA, 95 p.

Christie, W. J. 1973. A review of the changes in the fish species composition of Lake Ontario. Great Lakes Fish. Comm. Tech. Rep. 23: 65 p.

Clark, W. C., D. D. Jones, and C. S. Holling. 1979. Lessons for ecological policy design: a case study of ecosystem management. Ecol. Model. 7: 1–53.

Eschmeyer, P. H. 1955. The reproduction of lake trout in southern Lake Superior. Trans. Am. Fish. Soc. 84: 47–74.

Farmer, G. J. 1980. Biology and physiology of feeding in adult lampreys. Can. J. Fish. Aquat. Sci. 37: 1751–1761.

Heinrich, J. W., J. G. Weise, and B. R. Smith. 1980. Changes in biological characteristics of the sea lamprey (*Petromyzon marinus*) as related to lamprey abundance, prey abundance, and sea lamprey control. Can. J. Fish. Aquat. Sci. 37: 1861–1871.

Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can. Entomol. 91: 293–320.

[ed.] 1978. Adaptive environmental assessment and management. John Wiley and Sons. Chichester, England. 377 p.

Holling, C. S., C. J. Walters, and D. Ludwig. 1979. Surprise in resource and environmental systems. Int. Inst. Appl. Syst. Analysis, Res. Rep. Ser. (In press)

Jones, D. D. 1975. The application of catastrophe theory to ecological systems, p. 133–148. *In* G. S. Innis [ed.] New directions in the analysis of ecological systems, Part 2. Simulation Councils Inc., La Jolla, CA. (Also appeared in Simulation 29 (1): 1–15, 1977.)

Jones, D. D., and C. J. Walters. 1976. Catastrophe theory and fisheries regulation. J. Fish. Res. Board Can. 33: 2829–2833.

Lawrie, A. H. 1970. The sea lamprey in the Great Lakes. Trans. Am. Fish. Soc. 99: 766–775.

Lawrie, A. H., and W. MacCallum. 1980. On evaluating measures to rehabilitate lake trout (*Salvelinus namaycush*) of Lake Superior. Can. J. Fish. Aquat. Sci. 37: 2057–2062.

Lawrie, A. H., and J. F. Rahrer. 1973. Lake Superior: a case history of the Lake and its fisheries. Great Lakes Fish. Comm. Tech. Rep. 19: 69 p.

Lett, P. F., F. W. H. Beamish, and G. J. Farmer. 1975. System simulation of the predator activities of sea lampreys (*Petromyzon marinus*) on lake trout (*Salvelinus namaycush*). J. Fish. Res. Board Can. 32: 623–631.

Moav, R., T. Bordy, and G. Hulata. 1978. Genetic improvement of fish populations. Science 201: 1090–1094.

Murdoch, W. W. 1973. The functional response of predators. J. Appl. Ecol. 10: 335–342.

Pycha, R. L. 1977. Changes in lake trout stocks in Lake Superior, 1976. Appendix III, 1977 Minutes of Great Lakes Fish. Comm., Lake Superior Committee, Milwaukee, WI. 3 p. (Mimeo)

Pycha, R. L. 1980. Changes in mortality of lake trout (*Salvelinus namaycush*) in Michigan waters of Lake Superior in relation to sea lamprey (*Petromyzon marinus*) predation, 1968–78. Can. J. Fish. Aquat. Sci. 37: 2063–2073.

Pycha, R. L., and G. R. King. 1975. Changes in the lake trout population of southern Lake Superior in relation to the fishery, the sea lamprey, and stocking, 1950–1970. Great Lakes Fish. Comm. Tech. Rep. 28: 34 p.

Rahrer, J. F. 1967. Growth of lake trout in Lake Superior before the maximum abundance of sea lampreys. Trans. Am. Fish. Soc. 96: 268–277.

Ricker, W. E. 1963. Big effects from small causes: two examples from fish population dynamics. J. Fish. Res. Board Can. 20: 257–264.

Sakagawa, G. T., and R. L. Pycha. 1971. Population biology of lake trout (*Salvelinus namaycush*) of Lake Superior before 1950. J. Fish. Res. Board Can. 28: 65–71.

Silliman, R. P. 1969. Analog computer simulation and catch forecasting in commercially fished populations. Trans. Am. Fish. Soc. 99: 560–569.

Smith, B. R. 1971. Sea lampreys in the Great Lakes of North America, p. 207–247. *In* M. W. Hardesty and I. C. Potter [ed.] The biology of lampreys, Vol. I. Academic Press, New York, NY.

Smith, S. H. 1968. Species succession and fishery exploitation in the Great Lakes. J. Fish. Res. Board Can. 25: 667–693.

1972. The future of salmonid communities in the

Laurentian Great Lakes. J. Fish. Res. Board Can. 29: 951–957.

SWANSON, B. L., AND D. V. SWEDBERG. 1980. Decline and recovery of the Lake Superior Gull Island Reef lake trout (*Salvelinus namaycush*) population and the role of sea lamprey (*Petromyzon marinus*) predation. Can. J. Fish. Aquat. Sci. 37: 2074–2080.

WALTERS, C. J., AND R. HILBORN. 1978. Ecological optimization and adaptive management. Ann. Rev. Ecol. Syst. 9: 157–188.

WELLS, L. 1980. Lake trout (*Salvelinus namaycush*) and sea lamprey (*Petromyzon marinus*) populations in Lake Michigan, 1971–78. Can. J. Fish. Aquat. Sci. 37: 2047–2051.

WELLS, L., AND A. L. MCLAIN. 1973. Lake Michigan: man's effects on native fish stocks and other biota. Great Lakes Fish. Com:. Tech. Rep. 20: 55 p.

Appendix 1

Simplified Estimate of Juvenile Survival

A simple, minimum estimate of survival from egg to age 1 can be obtained as follows. The desired survival rate is

$$\text{(1a)} \quad S_o = N_1/E$$

where E is total egg production and N_1 is the number of survivors to age 1. For a population near equilibrium (i.e. Lake Superior before 1950), E can be expressed as

$$\text{(2a)} \quad E = 0.5\, N_1 S_a \sum_{i=a}^{\infty} S_m^{\,i-a} f_a$$

where S_a is *total* survival from age 1 to maturity at age a, S_m is the average *annual* survival rate of mature fish, and f_i is age specific fecundity. Each term of the sum in (2a) is just $N_i = N_1 S_a S_m^{\,i-a}$, the expected number of fish alive at age i, times fecundity. The factor of 0.5 accounts for a 50:50 sex ratio.

Combining (1a) and (2a), we get

$$\text{(3a)} \quad S_o = \frac{1}{0.5\, S_a \sum_{i=a}^{\infty} S_m^{\,i-a} f_i}$$

This equation implies that juvenile survival can be estimated even if total stock and egg production are unknown; the trick is to assume that the stock is near equilibrium.

From Sakagawa and Pycha (1971), S_m in Lake Superior was approximately 0.4 assuming age at maturity $a = 9$ yr. Using their body weight data and Eschmeyer's (1955) fecundity data, the following table can be constructed

Age, i	$s_m^{\,i-9}$	f_i
9	1.0	700
10	0.4	3000
11	0.16	4000
12	0.064	6000
13	0.026	9000
14	0.010	11000
15	0.004	13000
16	0.002	16000

(ages greater than 16 do not contribute significantly to the sum in eq. 3a). Summing the products of the second two columns and substituting into equation (3a),

$$\text{(4a)} \quad S_o = \frac{1}{(S_a)(1676)}$$

If the annual survival rate from age 1–9 was 0.8 (Sakagawa and Pycha 1971; Budd et al. 1969) and if fishing mortalities prior to age 9 are ignored, then $S_a = (0.8)^8 = 0.167$. Substituting this in equation (4a) gives $S_o = 0.004$, for a total survival from egg to maturity of 0.07%. This is only half the values of around 0.13–0.14% estimated by simulation and by Swanson and Swedburg (1980).

Estimates of Lamprey-Induced Mortality in Whitefish, *Coregonus clupeaformis*[1,2]

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SPANGLER, G. R., D. S. ROBSON, AND H. A. REGIER. 1980. Estimates of lamprey-induced mortality in whitefish, *Coregonus clupeaformis*. Can. J. Fish. Aquat. Sci. 37: 2146–2150.

The seasonal rate of lamprey attack upon lake whitefish in Lake Huron is estimable as the proportion of recently wounded fish in the catch. The nonfatal lamprey attack rate is estimable from the accumulation of healed scars observed on a cohort of marked (tagged) fish sampled throughout the fishing season. The difference between these estimates is an estimate of the fatal lamprey attack coefficient. In northern Lake Huron, lamprey attacks on whitefish are most frequent during August to November. The fatal lamprey attack rate is greatest during late summer when a large proportion of attacks results in the death of the host. Approximately 75% of the lamprey attacks on whitefish are fatal during mid-June to mid-November.

Key words: Lake Huron, *Petromyzon marinus*, lake whitefish, lamprey attack rate

SPANGLER, G. R., D. S. ROBSON, AND H. A. REGIER. 1980. Estimates of lamprey-induced mortality in whitefish, *Coregonus clupeaformis*. Can. J. Fish. Aquat. Sci. 37: 2146–2150.

Le taux saisonnier d'attaques de grandes lamproies marines sur le grand corégone dans le lac Huron peut être estimé comme proportion des poissons récemment blessés dans les prises. Le taux d'attaques non fatales peut être estimé d'après l'accumulation de cicatrices guéries sur une cohorte de poissons marqués (étiquetés) tout au long de la saison de pêche. La différence entre ces estimations est une estimation du coefficient d'attaques fatales par la grande lamproie marine. Dans la partie nord du lac Huron, les attaques de grandes lamproies marines sur le grand corégone ont une fréquence maximale entre août et novembre. Le taux d'attaques fatales par les lamproies est maximal à la fin de l'été, alors qu'une forte proportion des attaques entraînent la mort de l'hôte. Environ 75% des attaques de lamproies sur le grand corégone sont fatales entre la mi-juin et la mi-novembre.

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THIS paper presents estimates of lake whitefish (*Coregonus clupeaformis*) mortality induced by feeding attacks of sea lamprey (*Petromyzon marinus*) in northern Lake Huron. The estimation problem is confounded by the difficulty of observing the lamprey attack and feeding process in large bodies of water. Fish which are killed during an attack are "unobservable" in the sense that they simply fall to the bottom of the lake. Fish which are caught in the netting operations of commercial fishermen and which bear open wounds at the time of capture may not be readily assigned to the alternate categories of "killed by attack" or "survivor of attack" simply because the capture process of the fishery interrupts the feeding of the lamprey or the recovery (healing) process of the host fish. The only observable category of lamprey-marked fish in the catch upon which there is reasonable agreement among biologists as to the state of health of the host is that group of fish carrying scars (healed wounds). These fish have obviously survived lamprey attacks and may provide some hope of estimating (by

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subtraction) the fatal lamprey attack rate if the total lamprey attack rate is known.

Estimation of the Instantaneous Rate of Lamprey Attack

A stock of tagged whitefish in northern Lake Huron (Burnt Island fishery) provided an opportunity to estimate the nonfatal lamprey attack rate (Spangler 1974). Unmarked fish tagged and released from pound nets on one occasion and carrying a lamprey attack scar upon subsequent recapture provide the basis for estimating the nonfatal component of lamprey attack.

The method adopted to estimate the lamprey attack rate is based upon a model developed by Robson (1970) which assumes that the total attack coefficient is the simple sum of the fatal attack rate and the nonfatal attack rate. A nonfatal attack at any point in time is assumed not to alter the fish's probability of survival or of being subjected to additional attacks by lampreys. Robson (1970) refers to this as a Markov model of lamprey predation with nonstationary attack rates and survival rates:

$$\lambda(t) = \lim_{\Delta t \to 0} \frac{1 - \Pr\,[\text{not attacked during } (t, t + \Delta t)]}{\Delta t}$$

and

$$\lambda(t) = [1 - s(t)]\lambda(t) + s(t)\lambda(t)$$

where Pr denotes "probability of" and where $\lambda(t)$ is the instantaneous lamprey attack rate on a randomly chosen fish from any specified cohort and $s(t)$ is the conditional probability of surviving a lamprey attack.

An estimate of the total attack rate is given by the ratio:

$$\hat{\lambda}(t) = \frac{\omega_t}{\nu_t}$$

where ω_t is the number of whitefish caught at time t bearing one fresh lamprey mark and no other recent wounds, and ν_t is the total number of whitefish caught at time t with no recent lamprey wounds. The counts ω_t and ν_t may include whitefish bearing lamprey attack marks classed as "healed lamprey marks" as it is assumed that the fish have recovered from earlier attacks. It is also assumed that $\lambda(t)$ is a slowly changing function of t; in particular, the change over a period of time between lamprey attack and wound healing is assumed negligible.

The nonfatal lamprey attack rate is estimable from recapture records of fish tagged and subsequently examined for the presence of healed lamprey marks. The accumulated number of scars over the interval between tagging and subsequent recapture is a sufficient statistic for the Poisson model developed by Robson (1970). The model specifies that for any recaptured fish, the number of additional scars acquired is a Poisson random variable with an expected value given by the integral $[A(t)]$ of the product $a(t) = s(t)\lambda(t)$, integrated over the release-to-recapture interval. Among n such fish released at t_0 and recaptured at t_1 the total number s of additional scars is then also Poisson distributed; and the mean number per fish, $y = s/n$, is an estimate of

$$A(t_1) - A(t_0) = \int_{t_0}^{t_1} s(t)\lambda(t)\,dt.$$

For the Burnt Island whitefish data the pound netting season was arbitrarily divided into unit time intervals of 4 wk:

t_5 (May 19–June 15)
t_6 (June 16–July 13)
t_7 (July 14–Aug. 10)
t_8 (Aug. 11–Sept. 7)
t_9 (Sept. 8–Oct. 5)
t_{10} (Oct. 6–Nov. 10)

where t_i may be interpreted as the midpoint of the indicated time interval. The parameters of the model were then defined:

$$\theta_1 = A(t_6) - A(t_5)$$
$$\theta_2 = A(t_7) - A(t_6)$$
$$\theta_3 = A(t_8) - A(t_7)$$
$$\theta_4 = A(t_9) - A(t_8)$$
$$\theta_5 = A(t_{10}) - A(t_9).$$

The resultant estimates, $\hat{\theta}_1, \ldots, \hat{\theta}_6$, represent the average instantaneous rates of nonfatal lamprey attacks occurring on the specified cohort of whitefish during each of the unit time intervals defined above (Table 1). Note that $\hat{\theta}_5$ estimates the average attack rate over a 5-wk (rather than 4-wk) interval to accommodate the last few days of the normal pound net season. Since the assumption of Poisson variability was open to question, regression methods were used rather than the more efficient but less robust maximum likelihood estimation procedures. Estimates of the instantaneous rate of fatal lamprey attacks were then obtained by subtraction of the nonfatal attack estimate ($\hat{\theta}_i$) from the total attack estimate ($\hat{\lambda}_i$) for corresponding time intervals.

Results

NONFATAL LAMPREY ATTACK COEFFICIENTS

The nonfatal lamprey attack coefficients were estimated in a five-parameter regression model for t_6–t_{10} using data combined from whitefish age-classes 3 through 5. This model, fitted with weights proportional to sample size, accounted for 55% of the variability in the data (Table 2).

ESTIMATES OF TOTAL LAMPREY ATTACK COEFFICIENTS

The frequency in the catch of whitefish bearing a single fresh lamprey mark and no other recent wounds was summarized across all years for age-classes 3–5

TABLE 1. Design of the five-parameter model for estimating the nonfatal attack coefficients for unit time intervals during the pound net season.

Release interval i	Recapture interval j				
	6	7	8	9	10
5	θ_1	$\theta_1+\theta_2$	$\theta_1+\theta_2+\theta_3$	$\theta_1+\theta_2+\theta_3+\theta_4$	$\theta_1+\theta_2+\ldots+\theta_5$
6		θ_2	$\theta_2+\theta_3$	$\theta_2+\theta_3+\theta_4$	$\theta_2+\theta_3+\ldots+\theta_5$
7			θ_3	$\theta_3+\theta_4$	$\theta_3+\theta_4+\theta_5$
8				θ_4	$\theta_4+\theta_5$
9					θ_5

TABLE 2. Input data, X and Y matrices, and weighted regression results for estimates of the nonfatal lamprey attack rate.

				Y matrix	X matrix				
i	j	n_{ij}	s_{ij}	s_{ij}/n_{ij}	θ_1	θ_2	θ_3	θ_4	θ_5
5	6	171	0	0	1	0	0	0	0
5	7	85	1	0.0118	1	1	0	0	0
5	8	12	1	0.0833	1	1	1	0	0
5	9	16	1	0.0625	1	1	1	1	0
5	10	15	3	0.2000	1	1	1	1	1
6	7	314	14	0.0446	0	1	0	0	0
6	8	67	8	0.1194	0	1	1	0	0
6	9	54	7	0.1296	0	1	1	1	0
6	10	51	6	0.1176	0	1	1	1	1
7	8	48	6	0.1250	0	0	1	0	0
7	9	33	1	0.0303	0	0	1	1	0
7	10	22	3	0.1364	0	0	1	1	1
8	9	9	2	0.2222	0	0	0	1	0
8	10	6	0	0	0	0	0	1	1
9	10	8	0	0	0	0	0	0	1

Results:
$\hat{\theta}^T = (-0.0074, 0.0339, 0.0828, -0.0049, 0.0298)$
Weighted residual mean square = 0.0830 with 10 df
Multiple correlation coefficient = 0.7447

(Table 3). Observations of tagged fish in age-classes 4 and 5 were not sufficient to provide separate estimates of the lamprey attack coefficients for each age-class, so the data for ages 3 through 5 were combined to provide estimates of the total, fatal, and nonfatal lamprey attack coefficients (Table 4). These results may somewhat over- or under-estimate the actual attack coefficients applicable to individual age-groups due to the size-selective nature of lamprey predation.

A large proportion of summer–fall lamprey attacks on whitefish of ages 3–5 result in the death of the fish. Summing the nonfatal and total lamprey attack coefficients over the June–November period and expressing the result as a percentage indicates that 75% of the lamprey attacks on whitefish during this period are fatal.

In the context of other factors of mortality operating on the whitefish stock, we used estimates of the total instantaneous mortality for age-groups 3–5 ($Z = 1.7243$) and fishing mortality ($F = 0.0719$) based upon the tagged fish (Spangler 1974). The instantaneous fatal lamprey attack coefficient ($\hat{L}_{6-9} = 0.3388$) for the same time period ($t = 6$–9 in Table 4) amounts to ~20% of the total.

In terms of conditional mortality rates, lamprey predation would account for a 29% mortality over this period in the absence of other mortality factors. The conditional mortality rate for all nonfishing sources of mortality then is 81%, or slightly more than twice the conditional annual rate calculated by Cucin and Regier (1966) for southern Georgian Bay. The magnitude of this estimate clearly indicates that lamprey predation is a major source of mortality on adult whitefish in the northern waters of the main basin of Lake Huron.

Discussion

Estimates of the total lamprey attack coefficients

TABLE 3. Frequency of freshly wounded whitefish of age-classes 3–5 in the commercial catch at Burnt Island from 1964 to 1967.

Interval (t)	Parameter	Age-class				Ages 3–5 ω_t/ν_t
		3	4	5	3–5 (combined)	
5	ω	6	31	3	40	0.0143
	ν	631	1951	208	2790	
6	ω	5	8	5	18	0.0042
	ν	2071	1999	225	4295	
7	ω	123	54	11	188	0.0411
	ν	2961	1458	153	4572	
8	ω	299	131	23	453	0.2083
	ν	1431	643	101	2175	
9	ω	204	219	28	451	0.2019
	ν	1171	936	127	2234	
10	ω	86	125	21	232	0.1340
	ν	803	809	119	1731	

depend heavily upon the assumption that a nonfatal attack at any point in time does not influence the fish's chance of additional lamprey attacks. Lennon (1954) noted in his aquarium studies that the struggling of a fish under attack apparently made it more subject to additional lamprey attacks. Parker and Lennon (1956) observed, however, that although several lampreys may attach to a single prey fish, not all of the lampreys necessarily feed on that fish. Farmer and Beamish (1973) carefully examined the distribution of single and multiple attacks on white suckers (*Catostomus commersoni*) of similar size and concluded that the attachment of one or more lampreys on an individual fish did not influence additional attacks on that fish. If this is true also for lake whitefish then the major assumption of the lamprey attack estimation model is fulfilled.

It is not at all clear why sea lamprey predation is such a conspicuous component of mortality in Great Lakes fishes. Fry (1953) demonstrated the impact of lampreys on lake trout (*Salvelinus namaycush*) in South Bay of Lake Huron and lamprey predation is thought to have been a contributing source of mortality for white suckers (Hall and Elliott 1954; Coble 1967), rainbow trout, *Salmo gairdneri* (Berst and Wainio 1967), splake, *Salvelinus namaycush* × *S. fontinalis* (Berst and Spangler 1970; Spangler and Berst 1976), and the larger species of deep-water coregonines (Smith 1968) in Lake Huron.

TABLE 4. Estimates of the seasonal instantaneous lamprey attack coefficients, total ($\hat{\lambda}_t$), nonfatal ($\hat{\theta}_t$), and fatal ($\hat{L}_t = \hat{\lambda}_t - \hat{\theta}_t$), based on age 3–5 whitefish sampled from the commercial catch at Burnt Island from 1964 to 1967.

t	Lamprey attack coefficient		
	Nonfatal ($\hat{\theta}_t$)	Fatal ($\hat{L}_t$)	Total ($\hat{\lambda}_t$)
6	−0.0074[a]	0.0042	0.0042
7	0.0339	0.0072	0.0411
8	0.0828	0.1255	0.2083
9	−0.0049[a]	0.2019	0.2019
10	0.0298	0.1042	0.1340

[a] Negative values of the nonfatal attack coefficient are not meaningful and are treated as zero in all subsequent calculations.

The apparent coexistence of lake trout and sea lampreys in Seneca and Cayuga lakes (Royce 1950; Wigley 1959; Youngs 1980) and in Lake Ontario (Christie and Kolenosky 1980) is in strong contrast to the serious decimation of trout stocks in the upper Great Lakes (Lawrie 1970; Pycha 1980; Wells and McLain 1972). Lamprey parasitism has been reported on the whitefish of Loch Leven and Loch Lomond [both *P. marinus* (Slack 1955) and *Lampetra fluviatilis* (Maitland 1980)] and Great Slave Lake [*Entosphenus japonicus* (Rawson 1951)], but is not thought to be a source of significant mortality for these stocks. Lamprey attacks (*E. tridentatus* in Pacific and *P. marinus* in Atlantic regions) on salmon have been noted on both sides of the Pacific (Williams and Gilhousen 1968; Birman 1950) and on landlocked Atlantic salmon, *Salmo salar*, in Maine (Davis 1967). The latter accounts include wounding incidence as high as 85% although no appreciable mortality of prey fish is thought to have occurred.

In view of the conflicting evidence (most of which is apparently well-founded), it seems reasonable to assume that sea lampreys do act as true predators in those systems which have been sufficiently "softened up" in the sense of Regier and Loftus (1972) by extrinsic stresses. Systems in which lampreys have evolved or have been long-term residents may have sufficient community structure that lampreys are effectively confined to a parasitic role.

We suspect that some feedback mechanism in the predator–prey interaction operates at the level of individual feeding attacks in such a manner that the lamprey feeding rate (and concomitant host mortality) is influenced by the physiological state of the host fish. If this mechanism is a covariate of growth rate (known to be density-dependent and responsive to changes in fishery exploitation), then we might expect host fish which are growing most rapidly to be most likely to succumb to a single lamprey attack. This hypothesis is consistent with observations on the relatively slow-growing lake trout of Cayuga Lake (Youngs 1980) and lake whitefish of southern Georgian Bay (Spangler and Collins 1980).

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BERST, A. H., AND A. A. WAINIO. 1967. Lamprey parasitism of rainbow trout in southern Georgian Bay. J. Fish. Res. Board Can. 24: 2539–2548.

BERST, A. H., AND G. R. SPANGLER. 1970. Population dynamics of F_1 splake (*Salvelinus fontinalis* × *S. namaycush*) in Lake Huron. J. Fish. Res. Board Can. 27: 1017–1032.

BIRMAN, I. B. 1950. Parasitism of salmon of the genus *Oncorhynchus* by the pacific lamprey. Izv. TINRO 32: 158–160. Fish. Res. Board Can. Trans. Ser. 290: 3 p.

CHRISTIE, W. J., AND D. P. KOLENOSKY. 1980. Parasitic phase of the sea lamprey (*Petromyzon marinus*) in Lake Ontario. Can. J. Fish. Aquat. Sci. 37: 2021–2038.

COBLE, D. W. 1967. The white sucker population of South Bay, Lake Huron, and effects of the sea lamprey on it. J. Fish. Res. Board Can. 24: 2117–2136.

CUCIN, D., AND H. A. REGIER. 1966. Dynamics and exploitation of lake whitefish in southern Georgian Bay. J. Fish. Res. Board Can. 23: 221–274.

DAVIS, R. M. 1967. Parasitism by newly-transformed anadromous sea lampreys on landlocked salmon and other fishes in a coastal Maine lake. Trans. Am. Fish. Soc. 96: 11–16.

FARMER, G. J., AND F. W. H. BEAMISH. 1973. Sea lamprey (*Petromyzon marinus*) predation on freshwater teleosts. J. Fish. Res. Board Can. 30: 601–605.

FRY, F. E. J. 1953. The 1944 year class of lake trout in South Bay, Lake Huron. Trans. Am. Fish. Soc. 82: 178–192.

HALL, A. E. JR., AND O. R. ELLIOTT. 1954. Relationship of length of fish to incidence of sea lamprey scars on white suckers, *Catostomus commersoni*, in Lake Huron. Copeia 1954 (1): 73–74.

LAWRIE, A. H. 1970. The sea lamprey in the Great Lakes. Trans. Am. Fish. Soc. 99: 766–775.

LENNON, R. E. 1954. Feeding mechanism of the sea lamprey and its effect on host fishes. U.S. Fish Wildl. Serv. Fish. Bull. 98: 247–293.

MAITLAND, P. S. 1980. Scarring of whitefish (*Coregonus lavaretus*) by European river lamprey (*Lampetra fluviatilis*) in Loch Lomond, Scotland. Can. J. Fish. Aquat. Sci. 37: 1981–1988.

PARKER, P. S., AND R. E. LENNON. 1956. Biology of the sea lamprey in its parasitic phase. U.S. Fish. Wildl. Serv. Res. Rep. 44: 32 p.

PYCHA, R. L. 1980. Changes in mortality of lake trout (*Salvelinus namaycush*) in Michigan waters of Lake Superior in relation to sea lamprey (*Petromyzon marinus*) predation, 1968–78. Can. J. Fish. Aquat. Sci. 37: 2063–2073.

RAWSON, D. S. 1951. Studies of the fish of Great Slave Lake. J. Fish. Res. Board Can. 8: 207–240.

REGIER, H. A., AND K. H. LOFTUS. 1972. Effects of fisheries exploitation on salmonid communities in oligotrophic lakes. J. Fish. Res. Board Can. 29: 959–968.

ROBSON, D. S. 1970. Estimation of instantaneous lamprey attack rate. (Based on a Markov model of lamprey predation with non-stationary attack rates and survival rates.) Biometrics Unit Mimeo Ser. BU-276-M: 19 p. Cornell University, Ithaca, NY.

ROYCE, W. F. 1950. The effect of lamprey attacks upon lake trout in Seneca Lake, New York. Trans. Am. Fish. Soc. 79: 71–76.

SLACK, H. D. 1955. Factors affecting the productivity of *Coregonus clupeoides* Lacepede in Loch Lomond. Proc. Int. Assoc. Theor. Appl. Limnol. 12: 183–186.

SMITH, S. H. 1968. Species succession and fishery exploitation in the Great Lakes. J. Fish. Res. Board Can. 25: 667–693.

SPANGLER, G. R. 1974. Mortality factors and dynamics of a Lake Huron lake whitefish population. Ph.D. thesis, Department of Zoology, Univ. Toronto, Toronto, Ont.

SPANGLER, G. R., AND A. H. BERST. 1976. Performance of lake trout (*Salvelinus namaycush*) backcrosses, F_1 splake (*S. fontinalis* × *S. namaycush*), and lake trout in Lake Huron. J. Fish. Res. Board Can. 33: 2402–2407.

SPANGLER, G. R., AND J. J. COLLINS. 1980. Response of lake whitefish (*Coregonus clupeaformis*) to the control of sea lamprey (*Petromyzon marinus*) in Lake Huron. Can. J. Fish. Aquat. Sci. 37: 2039–2046.

WELLS, L., AND A. L. MCLAIN. 1972. Lake Michigan: effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 889–898.

WIGLEY, R. L. 1959. Life history of the sea lamprey of Cayuga Lake, New York. U.S. Fish. Wildl. Serv. Fish. Bull. 154: 561–617.

WILLIAMS, I. V., AND P. GILHOUSEN. 1968. Lamprey parasitism of Fraser River sockeye and pink salmon during 1967. Int. Pac. Salmon Fish. Comm., New Westminster, B.C. Prog. Rep. 18: 22 p.

YOUNGS, W. D. 1980. Estimate of lamprey-induced mortality in a lake trout (*Salvelinus namaycush*) population. Can. J. Fish. Aquat. Sci. 37: 2151–2158.

Estimate of Lamprey-Induced Mortality in a Lake Trout (*Salvelinus namaycush*) Population[1]

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YOUNGS, W. D. 1980. Estimate of lamprey-induced mortality in a lake trout (*Salvelinus namaycush*) population. Can. J. Fish. Aquat. Sci. 37: 2151–2158.

A competing risk model was applied to mortality occurring in a lake trout population subjected to fishing and lamprey parasitism. Two indices are proposed as a measure of lamprey-induced mortality in the lake trout (*Salvelinus namaycush*) population: the average number of wounds per fish (W/F) and the average number of scars per fish (S/F) accumulated by a cohort over a period of 1 yr. These indices were used as a measure of the force of lamprey-induced mortality. Fishing mortality was estimated from angler returns of tags on lake trout. Tag returns were also used in a maximum likelihood method to estimate survival of lake trout. Fishing and lamprey-induced mortality components of the model were analyzed by linear regression methods with the force of total mortality (i) as the independent variable. The component for lamprey-induced mortality (either W/F or S/F) did not contribute significantly to the reduction in variation of the force of total mortality, but the component for fishing mortality was significant. A negative coefficient for some analyses associated with the component for lamprey-induced mortality suggested a possible conditioning influence by other factors. Growth of lake trout was examined as a possible conditioning factor but analyses suggested that growth did not influence survival. Lamprey did not apparently cause any appreciable mortality in the lake trout population, age 4 and older, in Cayuga Lake during the years studied. It was not possible to consider younger age-groups of lake trout.

Keywords: lake trout, lamprey, mortality

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Un modèle de risques concurrentiels a été appliqué à la mortalité chez une population de touladis soumise à la pêche et à la prédation des lamproies. Nous proposons deux indices de mortalité provoquée par les lamproies chez la population de touladis (*Salvelinus namaycush*) : le nombre moyen des blessures par poisson (W/F) et le nombre moyen des cicatrices par poisson (S/F) accumulées par une cohorte sur une période d'un an. Ces indices ont été utilisés comme mesure de l'ampleur des mortalités provoquées par les lamproies. La mortalité par pêche est estimée à partir de retours d'étiquettes de touladis signalés par les pêcheurs à la ligne. Les retours d'étiquettes ont été également utilisés comme méthode de probabilité maximale dans l'estimation de la survie des touladis. Les éléments pêche et mortalité provoquée par les lamproies dans le modèle ont été analysés par régression linéaire, l'ampleur de la mortalité totale (i) étant la variable indépendante. L'élément mortalité provoquée par les lamproies (W/F ou S/F) n'a pas contribué de façon marquée à réduire la variation de l'ampleur de la mortalité totale, alors que l'élément mortalité par pêche était significatif. Un coefficient négatif dans certaines analyses, associé à l'élément mortalité provoquée par les lamproie suggère un conditionnement possible par d'autres facteurs. Nous avons examiné la croissance du touladi comme facteur de conditionnement possible, mais les analyses laissent penser que la croissance n'affecte pas la survie. La lamproie ne semble pas avoir causé de mortalités appréciables chez la population de touladis, d'âge 4 et plus, dans le lac Cayuga dans les années étudiées. Il a été impossible d'étudier les groupes d'âge plus jeunes de touladis.

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THE sea lamprey (*Petromyzon marinus*) has been credited with the decline of many fish populations in the Great Lakes (Hile et al. 1951a, b; Fry 1953; Eschmeyer 1957; and Moffett 1958 for example). Sea lamprey in certain inland waters exert little apparent effect on similar fish communities (Royce 1950; Webster et al. 1959; Youngs and Oglesby 1972) and this poses an anomalous situation.

The objective of this study was to partition mortality observed in a population of lake trout into three causes: fishing, lamprey-induced, and remaining or other

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natural causes. There is virtually no published information on the force of lamprey-induced mortality in fish populations although a series of publications concerning lake trout in South Bay, Lake Huron, relate lamprey marks observed on lake trout to lake trout mortality (Fry 1953; Fry and Budd 1958; Budd and Fry 1960; Budd et al. 1969). Spangler and Collins (1980) demonstrated the seasonal levels of lamprey-induced mortality on whitefish in Lake Huron.

Several inland lakes of New York containing both lamprey and salmonid populations could provide excellent opportunities for studying the interactions of lamprey and lake trout. Cayuga Lake is particularly well suited for several reasons. There exists an extensive body of relevant data as the result of long-term studies on the lake (Webster et al. 1959). The lake trout population is maintained by annual stocking that is finclipped and, thus, provides a known-age population. Reproduction does not occur to any extent due to siltation of spawning sites (Webster et al. 1959). The lake trout population was successfully increased to the level of excellent sportfishing by stocking despite the presence of lamprey populations of approximately 5000–10 000 spawning adults (Wigley 1959).

The lamprey, of course, feeds on more than a single species. Surface (1899) listed 28 species that had been attacked in Cayuga Lake. Lampreys may have preference for a particular prey species, feeding may be conditioned by past feeding history, or attack may be on the basis of random encounters with an acceptable host. The determination of such factors will not be possible in the present study and an assumption will be made that other species serving as hosts for the lamprey have remained in a somewhat constant state. It is known that the lake trout population showed a marked increase during the early 1940s and that the rainbow trout showed an increase in the early 1960s. The extent that these species have altered the biological system of Cayuga Lake is not known.

Materials and Methods

COMPETING RISKS OF DEATH

The situation where there are two causes of death (fishing and natural) operating on a fish population assuming a deterministic model has been considered by Ricker (1948, 1958, 1975). The natural component includes all causes other than fishing and is generally assumed to be constant. Chiang (1968) has developed the competing risks of death model from a stochastic viewpoint. A stochastic model with three competing risks of death will be assumed in this study. The following definitions and notation will be used:

F = coefficient of fishing mortality
L = coefficient of lamprey-induced mortality
M = coefficient of natural mortality
Z = Coefficient of total mortality
S = probability of survival

It will be assumed that $Z = F + L + M$ and that $S = \exp\text{-}Z$.

ESTIMATING MORTALITY COMPONENTS

The lake trout population, age 4 and older, was sampled in October as the fish congregated off Taughannock Point during spawning. Trout were examined for wounds and scars, measured for length and weight, sexed, and tagged with a mandible ring tag. The sampling program has been described in detail by Webster et al. (1959) and Youngs (1972).

Total mortality — Survival, the compliment of total mortality, was estimated by the method developed independently by Seber (1970) and Robson and Youngs (1971) with further consideration by Youngs and Robson (1975). Briefly stated, if a series of tagged fish is released into a population over a period of years as an annual event, and a record kept of tags returned, survival can be estimated by the following:

$$\hat{S}_\kappa = \frac{M_{\kappa+1}}{M_\kappa} \cdot \frac{T_{\kappa+1} - R_{\kappa+1}}{R_{\kappa+1}} \cdot \frac{R_\kappa}{T_\kappa}$$

where

M_κ = number of individuals marked during the κth sample
R_κ = total recaptures reported from the κth marking.
T_κ = total number of recaptures reported after the κth sample that were marked on or before the κth sample.

Fishing mortality — Fishing mortality is measurable but it is not generally completely measured and, therefore, some indirect method of estimation is normally employed. Several methods of estimation of fishing mortality are available but assumptions concerning completeness must be made. The estimation of the expectation of death from fishing for a specified year is defined as the ratio of the number of fish caught during the year to the number of fish in the population at the start of that year. A minimum estimate of the expectation of death from fishing is provided by the ratio of the number of tags returned to the number of tags released prior to fishing in that year.

Robson and Youngs (1971) also developed a maximum likelihood estimator for reported expectation of death from fishing. From the same tag recapture sequence as described above, the maximum likelihood estimator for reported expectation of death from fishing is:

$$f_\kappa = \frac{R_\kappa}{M_\kappa} \cdot \frac{C_\kappa}{T_\kappa}$$

where R_κ, T_κ, and M_κ are as defined above, and C_κ = the number of tags reported for the κth year of fishing.

Lamprey-induced mortality — This study will consider scars and wounds on lake trout as an index of lamprey-induced mortality. Scars were considered to be any lamprey feeding site that had been sealed by epithelial tissue. A wound was defined as an open lesion caused by lamprey attack that had not been entirely sealed by epithelial tissue. The period of transition from wound to scar appears to have been of short duration since fish with questionable lamprey marks were not frequently encountered.

There is no direct way of estimating lamprey-induced death as is available for estimating fishing mortality. It becomes necessary to resort to some index of lamprey activity and relate this to mortality in the lake trout population. There would seem to be three measures that could be used for such an index; these are lamprey wounds, lamprey scars, and the number of lampreys.

Wounds in this study have been reported as wounds per fish as calculated from the total number of wounds observed divided by the number of trout in the sample. The observed wounds per fish have been weighted to correspond to the time interval of the survival estimate when the two periods were not concurrent. Details of the procedure and rationale have been given by Youngs (1972). Wounds per fish have been treated as an instantaneous measure and, therefore, are used untransformed in the model for forces of mortality.

Scars are cumulative with age of lake trout and, therefore, were determined on a lake trout year-class sample year basis. The scar index used was scars per fish determined from the number of observed scars divided by the number of lake trout in the sample. The natural logarithm of scars per fish index was used in the expression for forces of mortality.

Natural mortality — The remaining mortality or natural mortality is estimated as the difference between total and fishing plus lamprey-induced mortality. It is assumed in this study that the sum of forces of other mortalities treated as natural mortality remains constant, but that an individual force in this group may vary from year-to-year.

Analysis of Data

The following two models were analyzed by standard regression techniques; the first model corresponding to wounds per fish (W/F), and the second corresponding to scars per fish (S/F), as an index of lamprey-induced mortality:

$$Z = M + b_1 F + b_2 W/F \qquad Z = M + b_1 F + b_3 \log_2 S/F$$

The coefficients of b_1, b_2, and b_3 will have the following defined interpretation throughout the remainder of this study:

b_1 = a coefficient relating minimum force of fishing to force of fishing mortality

b_2 = a coefficient relating wounds per fish to force of lamprey-induced mortality

b_3 = a coefficient relating scars per fish to force of lamprey-induced mortality.

The sum of the forces of mortality other than forces of fishing and lamprey-induced mortality is assumed to remain constant.

Wounds as an index — Wounds per fish were weighted on the basis of 5/12 (months) for the value observed in the sample year plus 7/12 of the value observed for the following sample year. Analysis of the data in Table 1 gave the following relationship for forces of mortality:

$$Z = 0.605 + 5.715F - 0.905\ W/F$$

The contribution of fishing to the coefficient of total mortality was significant, accounting for 71.5%, but the contribution from the index of lamprey activity (wounds per fish) was not significant when fishing mortality was taken into account. The negative sign of the b_2 coefficient has no biological meaning in terms of the expressed model.

TABLE 1. Estimates of survival (S), expectation of death from fishing (E), coefficient of total mortality (Z), coefficient of fishing mortality (F), and wounds per fish (W/F) for lake trout taken in spawning population samples, Cayuga Lake, 1960–69.

Sample year	S	E	Z	F	W/F
1960–61	0.420	0.069	0.867	0.103	0.498
1961–62	0.475	0.092	0.744	0.130	0.588
1962–63	0.718	0.058	0.330	0.068	0.495
1963–64	0.481	0.071	0.732	0.100	0.576
1964–65	0.632	0.051	0.459	0.064	0.532
1965–66	0.450	0.071	0.798	0.103	0.429
1966–67	0.548	0.043	0.601	0.057	0.545
1967–68	0.696	0.056	0.362	0.067	0.602
1968–69	0.733	0.023	0.311	0.027	0.516

The b_1 coefficient of 5.715 represented an estimated angler return of tags of 17.5%. The average coefficient of fishing mortality during that time period would have been 0.457.

The relationship for coefficients of mortality excluding coefficient of lamprey-induced mortality from the model was:

$$Z = 0.127 + 5.645F$$

This regression accounts for 66.4% of the variation in Z and is significant ($F = 13.85$, df = 1, 7). The estimate for b_1 remains essentially the same but the estimate for the coefficient of natural mortality is reduced considerably (0.605 to 0.129).

Scars as an index — The increment of scars per fish observed between sample years on a year-class basis (Table 2) were averaged to obtain an estimate of the increase in scars per fish for a sample year. These average increments of scars per fish are given in Table 3 along with the corresponding survival and exploitation rates. There were fewer years information to work with since scars were not recorded for the 1965 spawning population sample. Therefore, the increments for 1964–65 and 1965–66 could not be determined.

The estimated regression equation for these data is:

$$Z = 0.199 + 4.389F - 0.102 \log_2 S/F$$

Analysis of variance for these data showed a nonsignificant contribution from regression.

Eliminating the index of lamprey activity from the model results in a significant contribution for regression ($F = 8.55$ with 1,5 df). The estimated regression was

$$Z = 0.149 + 5.257F$$

which gave an estimate of 0.415 for the coefficient of fishing mortality. The estimates for coefficient of natural mortality and coefficient of fishing mortality are in good agreement, which would be expected since force of lamprey-induced mortality is near zero.

The spawning population samples gave significant

TABLE 2. Observed average number of scars per fish by year-class and year samples for lake trout taken in spawning population samples, Cayuga Lake, 1960–69. Number of fish is given in parentheses. No scar information was collected for 1965.

	Sample year								
Year-class	1960	1961	1962	1963	1964	1966	1967	1968	1969
1950	2.800 (5)	3.250 (4)							
1951	4.357 (14)	4.273 (11)	5.286 (21)						
1952	3.090 (11)	3.400 (30)	4.500 (26)						
1953	3.125 (8)	3.885 (26)	4.440 (25)	6.833 (6)					
1954	2.429 (7)	3.207 (29)	3.500 (46)	4.714 (7)					
1955	1.750 (4)	2.071 (28)	1.875 (16)	4.308 (13)	5.481 (27)		3.429 (7)		
1956		2.600 (5)	2.667 (12)	2.769 (13)	5.682 (22)		4.900 (10)		
1957			2.250 (4)	3.579 (19)	4.106 (47)		4.358 (53)		
1958				3.333 (3)	3.667 (15)	1.333 (2)	3.792 (101)	4.288 (66)	5.640 (25)
1959						1.714 (7)	3.205 (229)	4.704 (54)	5.192 (26)
1960						2.667 (12)	3.404 (198)	4.339 (52)	4.841 (44)
1961						1.778 (9)	2.600 (90)	3.740 (96)	4.476 (82)
1962							2.063 (63)	3.348 (138)	3.809 (178)
1963							1.192 (26)	2.429 (7)	3.315 (92)
1964									2.973 (37)

TABLE 3. Estimates of survival (S), expectation of death from fishing (E), coefficient of total mortality (Z), coefficient of fishing mortality (F), and average increase in scars per fish (S/F) for lake trout taken in the spawning population samples, Cayuga Lake, 1960 to 1969.

Sample year	S	E	Z	F	S/F	ln (S/F)
1960–61	0.420	0.069	0.867	0.103	0.286	−1.252
1961–62	0.475	0.092	0.744	0.130	0.472	−0.751
1962–63	0.718	0.058	0.330	0.068	1.494	0.401
1963–64	0.481	0.071	0.732	0.100	1.237	0.213
1966–67	0.548	0.043	0.601	0.057	1.377	0.320
1967–68	0.696	0.056	0.326	0.067	1.099	0.094
1968–69	0.733	0.023	0.311	0.027	0.737	−0.305

relationships between force of total mortality and force of fishing mortality. This may be due, at least in part, to the correlation between survival and reported expectation of death from fishing resulting from the estimation procedure.

The index used for force of lamprey-induced mortality, either wounds or scars, did not contribute significantly to variation in force of total mortality. There are some tentative conclusions from this result. Lampreys caused very little mortality in the lake trout popu-

TABLE 4. Mean length (cm) for age 6 and 7, coefficient of growth (g), coefficient of total mortality (Z), coefficient of fishing mortality (F), and wounds per fish (W/F) for lake trout taken in spawning population samples, Cayuga Lake, 1960–69.

Sample year	Length (age 6)	Length (age 7)	g	Z	F	W/F
1960–61	64.85	66.73	0.029	0.867	0.103	0.498
1961–62	64.82	65.53	0.011	0.744	0.130	0.588
1962–63	64.11	67.01	0.044	0.330	0.068	0.495
1963–64	64.82	66.85	0.031	0.732	0.100	0.576
1964–65	65.23	67.62	0.036	0.459	0.064	0.532
1965–66	65.96	67.95	0.030	0.798	0.103	0.429
1966–67	66.09	67.62	0.023	0.601	0.057	0.545
1967–68	65.43	67.62	0.033	0.362	0.067	0.602
1968–69	66.42	67.64	0.018	0.311	0.027	0.516

lation studied if it is assumed that the model and estimates are valid. Alternatively, the indices used for lamprey-induced mortality did not represent lamprey-induced mortality, again assuming the model to be correct. The strongest conclusion would be that the model for mortality is incorrect. The strongest criticism against the model would be the assumption of constant "natural" mortality. The possible conditioning of survival by some means in the event of lamprey attack would be a reasonable addition to the model. This is considered next.

GROWTH AS A FACTOR CONDITIONING SURVIVAL

The physical condition of a lake trout at the time of lamprey attack could influence survival of the lake trout. A fish in good condition might have a greater chance of surviving a lamprey attack for two reasons. It should be able to survive the immediate attack better than a fish in poor condition. Secondly, an actively growing fish should be able to recover from attack better than a fish under poor growing conditions.

Two indicators of the physical condition of lake trout were used in this study. Growth, as measured by change in length of a year-class of lake trout between samples, was the first evaluated as a measure of physical well-being.

Mean lengths for the various age groups were also computed from the spawning population samples. As a measure of comparative growth between sample years, lengths of 6- and 7-yr old lake trout from the same year classes in consecutive sample years were chosen (Table 4). These ages were taken to obtain as large a sample size as available. The natural logarithm of the length at age $n + 1$ minus the natural logarithm at age n was taken as an estimate of the growth coefficient. Analysis of variance for the data in Table 4 again substantiate the conclusion that fishing is the only significant factor causing measurable changes in the force of total mortality. Including growth coefficients in the model caused an overall reduction of the variation observed in the force of total mortality but this reduction was not significant.

The relation between wounds per fish and weight at an arbitrary length was examined for the spawning population sample. This sample covers the least amount of time and, therefore, eliminates seasonal variation in condition to a large extent. It does have the tendency to exaggerate differences in condition between sexes. However, in attempting to break down the data by sex too few specimens resulted per category and, therefore, pooled information was used. The one category that was retained was number of wounds. Only those fish having no wounds were used to compute a length–weight relationship. This length–weight relationship was calculated on the basis of linear regression fitted to the logarithms of length and weight. A weight was then calculated for an arbitrary trout length of 66 cm. Analysis of these data showed no significant relationship ($r = 0.19$) between wounds per fish and weight for the given length of 66 cm. The condition of the lake trout as measured by weight for a given size apparently had no influence on the survival after lamprey attack.

Wigley (1959) found significant differences between weights of lake trout in Cayuga Lake having zero, one or two, or more wounds. His covariance analyses were on the basis of pooled standard gang samples since no difference was observed in length-weight relationship between sex of lake trout or sample year.

The spawning population samples were used in the present study to compare weight loss with number of wounds per fish. If lake trout condition is a factor influencing survival in the event of lamprey attack, a negative relationship should exist between weight loss and number of wounds per fish. A small weight loss should be less harmful to the fish (i.e. greater survival) and, therefore, greater numbers of wounds would be observed.

Length-weight relationships were calculated for lake trout having no wounds and one wound. These relationships were used to calculate the expected weight of a lake trout having no wounds and having one wound (Table 5). Weight loss was taken as the difference between the two calculated weights. Analysis of the data in Table 5 indicated no relationship be-

TABLE 5. Calculated weight in kilograms for 66-cm lake trout with no wound and one wound from data taken from spawning population samples, Cayuga Lake, 1962–69.

Year	Weight 0 wound	Weight 1 wound	Difference	*W/F*
1962	2.563 (131)[a]	2.508 (49)	0.054	0.674
1963	2.622 (48)	2.527 (17)	0.095	0.367
1964	2.740 (26)	2.527 (47)	0.213	0.726
1966	2.740 (145)	2.654 (47)	0.086	0.454
1967	2.631 (143)	2.617 (96)	0.014	0.610
1968	2.608 (422)	2.576 (194)	0.032	0.596
1969	2.522 (560)	2.522 (177)	0.000	0.459

[a] Number in parentheses is the sample size used in calculations of the length–weight relationship.

tween weight loss and number of wounds per fish (correlation coefficient = 0.32). Weight loss following lamprey attack was significant in all but one year; this substantiates the findings of Wigley (1959).

Growth of lake trout, as measured by the methods and with the degree of accuracy considered here, did not influence the effect of lamprey attack on lake trout survival.

Discussion

Evaluation of a specific cause of death, in particular that caused by the lamprey, is not a simple task. This was seen in the example of Cayuga Lake used in this study. It is necessary to be able to identify and have some index to measure each risk of death operating in the population. An accurate estimate of total mortality is also essential and requires careful consideration as to methods employed to obtain such estimates. The ecology of lake trout makes the problem more complex in that availability to certain types of gear becomes restricted. In considering indices to use for lamprey activity the choice is not great. Wounds seem the most obvious to use but several difficulties may be encountered. Wounding as a function of time in a natural situation is generally unknown although Robson's (1970) approach may be used to obtain an estimate of seasonal activity. Wounding levels may not reflect the same mortality from year to year if the fraction surviving attack is some function of time or size of fish and/or of lamprey. Scars have the same general restrictions and in addition must be considered on a year-class basis. Scars do reflect the accumulation of the wounding rate throughout the time period but may be affected by a changing rate of survival in the event of attack. In situations where adult spawning lamprey can be censused it may prove more practical to use their numbers as an index but in general this information would not be as readily obtained as scar or wound frequencies. The hypothesis set forth by Kitchell and Breck (1980) should be evaluated thoroughly before using wounds and scars as indices of lamprey-induced mortality. Their hypothesis is that the lamprey acts as either a predator at low host density or a parasite at high host density.

Cayuga Lake provides an example where a lake trout population has been increased to the point of providing a sport fishery of excellent quality even with the presence of lampreys. In this situation if the lamprey exercised such complete control over lake trout it would not have been possible for this to have happened. Size of the adult lamprey has frequently been stated as a factor accounting for the difference between the Cayuga Lake situations and the more recently established populations in the Great Lakes. Wigley (1959) gives the mean length from Cayuga and Seneca lakes and for two areas of Lake Huron, Carp Creek, and Ocqueoc River. The greatest difference in length is 2.29 cm for Cayuga Inlet (38.86) and Ocqueoc River (41.15). The greatest difference in weight was 40.5 g for Carp Creek (127.5) and Seneca Lake (168.0). Adult lamprey taken at the fishway trap on Cayuga Inlet in 1970 had an average length of 44.45 cm and an average weight of 255.0 g. Adult lampreys for the Ocqueoc River, Lake Huron, in 1970, had an average length of 43.18 cm and an average weight of 161.7 g (B. R. Smith, U.S. Fish and Wildlife, Marquette, MI, personal communication).

The complete lack of any significance in variation of mortality connected with an index of lamprey activity in the general model does not prove the lack of lamprey-induced mortality. As stated before, the model may be incorrect, estimates of the components may not be valid, or the host–parasite ratio may be in a region favoring low mortality (Kitchell and Breck 1980). One is tempted to accept the general concepts and utility of the model for mortality as it has been set forth by Ricker (1958) and Chiang (1968) particularly as it has been successfully applied in other situations, i.e. public health and human population work. The weakest part as used in this study would seem to be related to obtaining estimates and indices for mortality components. It is in this area that further refinement is needed.

In this study it has been possible to consider only the lake trout population 4 yr old and greater. Mortality in younger age-groups and caused by lamprey is not known. At present there does not seem to be a direct way of obtaining this information. If one constructs a catch curve using age 3 and older lake trout in Cayuga Lake as Webster et al. (1959) have done, a depression occurs at age 4. This depression could result from an increase in mortality at this age, perhaps due to lamprey, but for reasons stated in Youngs (1972) it is more likely due to entry into the sport-fishery and selectivity of gill nets.

The information derived from the spawning population samples taken in 1960 through 1970 seems to provide insight into the problem. The most informative, if we assume good estimates and an applicable model, was the lack of any significance due to lamprey activity. Coupled with this is an unexpected alteration of sign for this component. The reason for this is not at all apparent but two thoughts do arise. Youngs (1972) documented for a hypothetical example that such a relation could arise when the model did not account for all the mortality components in the population, in particular, if an unaccounted cause had values appreciably higher than the causes considered. The same result could occur if in fact some other factors conditioned survival, such that in a year of higher survival more lamprey-attacked trout did survive to be observed. The more obvious conditioning factor of growth did not show any relationship to survival. The host:parasite ratios could not be examined due to insufficient information.

Another result which lends supportive evidence to a low level of lamprey-induced mortality was the effect relatively small changes in reported exploitation had on force of total mortality. The reason for this would presumably be a less than complete reporting of tags by anglers. The b_1 regression coefficient for the force of fishing mortality was shown to be inversely related to the fraction of anglers who returned tags (Youngs 1974). The coefficients for the force of fishing mortality varied from 2.618 to 5.690 which corresponds to 38–18% anglers returning tags. This range of percent of anglers returning tags is very similar to percent of anglers returning tags from trout fisheries in California as reported by Butler (1962).

An inherent problem in the above regression procedure, for relating force of total mortality and force of fishing mortality, resulted when tag recapture returns were used as the basis for survival and exploitation estimates. This problem is the correlation between survival and exploitation when the same tag recapture information is used to estimate both components. However, similar b_1 coefficients resulted when using a different set of samples which resulted in independent estimates of survival and exploitation (Youngs 1972).

Immediate mortality of tagged lake trout would also give the same result as incomplete tag returns by anglers. Youngs and Robson (1975) provided a statistical test for this possibility. An analysis of spawning population tag return data resulted in nonsignificant chi-square values. The conclusion drawn from this was that the cause for the observed percentages of tag returns was the result of some anglers not returning tags.

A final, and convincing, argument against a devastating lamprey-induced mortality of lake trout in Cayuga Lake, over 4 yr old, is the presence of old, known-age fish. This evidence is nonrefutable due to the fin clipping and tagging program conducted on the lake trout population for the past 21 yr.

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Budd, J. C., and F. E. J. Fry. 1960. Further observations on the survival of yearling lake trout planted in South Bay, Lake Huron. Can. Fish Cult. 26: 7–13.

Budd, J. C., F. E. J. Fry, and P. S. M. Pearlstone. 1969. Final observations on the survival of planted lake trout in South Bay, Lake Huron. J. Fish. Res. Board Can. 26: 2413–2424.

Butler, R. L. 1962. Recognition and return of trout tags by California anglers. Calif. Fish Game 48(1): 5–18.

Chiang, C. L. 1968. Introduction to stochastic processes in biostatistics. John Wiley and Sons, Inc. New York, N.Y. 313 p.

Eschmeyer, P. H. 1957. The near extinction of lake trout in Lake Michigan. Trans. Am. Fish. Soc. 85: 102–119.

Fry, F. E. J. 1953. The 1944 year class of lake trout in South Bay, Lake Huron. Trans. Am. Fish. Soc. 82: 178–192.

Fry, F. E. J., and J. C. Budd. 1958. The survival of yearling lake trout planted in South Bay, Lake Huron. Can. Fish Cult. 23: 1–9.

Hile, R., P. H. Eschmeyer, and G. F. Lunger. 1951a. Decline of the lake trout fishery in Lake Michigan. U.S. Fish Wildl. Serv. Fish. Bull. 60: 77–95.

1951b. Status of the lake trout fishery in Lake Superior. Trans. Am. Fish. Soc. 80: 278–312.

Kitchell, J. F., and J. E. Breck. 1980. Bioenergetics model and foraging hypothesis for sea lamprey (*Petromyzon marinus*). Can. J. Fish. Aquat. Sci. 37: 2159–2168.

Moffett, J. W. 1958. Attack of the sea lamprey. Mich. Conserv. Mag. May–June. 6 p.

Ricker, W. E. 1948. Methods of estimating vital statistics of fish populations. Indiana Univ. Publ. Sci. Ser. 15: 101 p.

1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Can. 119: 300 p.

1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

Robson, D. S. 1970. Estimation of instantaneous lamprey attack rate. (Based on a Markov model of lamprey predation with non-stationary attack rates and survival rates.) Cornell Univ. Biom. Unit Mimeo Ser. BU-276-M: 19 p.

Robson, D. S., and W. D. Youngs. 1971. Statistical analysis of reported tag recaptures in the harvest from an exploited population. Cornell Univ. Biom. Unit Mimeo Ser. BU-369-M: 15 p.

Royce, W. F. 1950. The effect of lamprey attacks upon lake trout in Seneca Lake, New York. Trans. Am. Fish. Soc. 79: 71–76.

Seber, G. A. F. 1970. Estimating time-specific survival and reporting rates for adult birds from band returns. Biometrika 57(2): 313–318.

Spangler, G., and J. J. Collins. 1980. Response of lake whitefish (*Coregonus clupeaformis*) to the control of sea lamprey (*Petromyzon marinus*) in Lake Huron. Can. J. Fish. Aquat. Sci. 37: 2039–2046.

SURFACE, H. A. 1899. Removal of lampreys from the interior waters of New York. 4th Annu. Rep. Comm. Fish. Game Forests. p. 191–245.

WEBSTER, D. A., W. G. BENTLEY, AND J. P. GALLIGAN. 1959. Management of the lake trout fishery of Cayuga Lake, with special reference to the role of hatchery fish. Cornell Univ. Agric. Exp. Stn. Mem. 357: 83 p.

WIGLEY, R. L. 1959. Life history of the sea lamprey of Cayuga Lake, New York. U.S. Fish. Wildl. Serv. Fish. Bull. 154: 561–617.

YOUNGS, W. D. 1972. An estimation of lamprey-induced mortality in a lake trout population. Ph.D. Thesis, Cornell Univ., Ithaca, N.Y. 148 p.

1974. Estimation of the fraction of anglers returning tags. Trans. Am. Fish. Soc. 103: 616–618.

YOUNGS, W. D., AND R. T. OGLESBY. 1972. Cayuga Lake: effects of exploitation and introductions on the salmonid community. J. Fish. Res. Board Can. 29: 787–794.

YOUNGS, W. D., AND D. S. ROBSON. 1975. Estimating survival rate from tag returns: model tests and sample size determinations. J. Fish. Res. Board Can. 32: 2365–2371.

Bioenergetics Model and Foraging Hypothesis for Sea Lamprey (*Petromyzon marinus*)[1]

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KITCHELL, J. F., AND J. E. BRECK. 1980. Bioenergetics model and foraging hypothesis for sea lamprey (*Petromyzon marinus*). Can. J. Fish. Aquat. Sci. 37: 2159–2168.

A bioenergetics model for growth of lamprey during the parasitic phase was used to estimate food consumption by lampreys and the impact of lamprey feeding on host fishes. Estimates are evaluated by application to several Great Lakes case histories. Temperature and size-dependence of feeding and respiration were sufficient to account for growth dynamics. The model demonstrates that distribution of host fishes, by determining the thermal history of the lamprey, has important effects on lamprey life history and host mortality. Modeled lamprey growth and feeding rates, relative to size of the host, predict a strongly seasonal host mortality rate peaking in autumn. The predicted mortality pattern corresponds with that of independently derived data. Principles of optimal foraging theory applied to lamprey yield a hypothesis that predicts highest wounding and scarring frequencies at intermediate lamprey: host abundance ratios. A second component of the hypothesis predicts seasonal changes in these frequencies as lamprey size increases. Growth rates of lamprey and their host species plus wounding and scarring frequencies are more sensitive indicators of changing abundance ratios and lamprey effects than population changes resulting from predation by lamprey.

Key words: sea lamprey, *Petromyzon marinus*; model, bioenergetics, growth, consumption, fish mortality, Great Lakes

KITCHELL, J. F., AND J. E. BRECK. 1980. Bioenergetics model and foraging hypothesis for sea lamprey (*Petromyzon marinus*). Can. J. Fish. Aquat. Sci. 37: 2159–2168.

Un modèle bioénergétique de croissance de la grande lamproie marine durant la phase parasitaire a été utilisé pour estimer la consommation de nourriture et l'impact de l'alimentation de cette espèce sur les poissons hôtes. L'application du modèle à plusieurs dossiers des Grands Lacs a servi à évaluer ces estimations. La température et l'influence de la taille sur la nourriture et la respiration suffisent à expliquer la dynamique de la croissance. D'après le modèle, la distribution des poissons hôtes, qui détermine le passé thermique de la grande lamproie marine, a une influence marquée sur le cycle biologique de la lamproie et sur la mortalité de l'hôte. Les taux de croissance et de nutrition de la grande lamproie marine, modélisés par rapport à la taille de l'hôte, font prévoir un taux de mortalité des hôtes fortement saisonniers, avec pic en automne. La mortalité prédite s'accorde avec celle de données déduites indépendamment. Les principes de la théorie d'une quête optimale de nourriture, appliqués à la lamproie, conduisent à une hypothèse qui prévoit des fréquences maximales de blessures et de cicatrices à des rapports intermédiaires d'abondance lamproies:hôtes. Un second élément de l'hypothèse prévoit des changements saisonniers de ces fréquences à mesure qu'augmente la taille des lamproies. Le taux de croissance des lamproies et de leurs espèces proies, en plus de la fréquence des blessures et des cicatrices, sont des indicateurs plus sensibles des changements dans les rapports d'abondance et des effets du parasite que ne le sont les changements dans la population par suite de la prédation par la lamproie.

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THE purpose of this paper is to describe and apply a bioenergetics model of sea lamprey growth during the parasitic phase. This model employs the physiological processes of energy budgeting as the basis for assessing amounts of food consumed by lampreys, lamprey thermal distribution and life history, and the effects of lamprey parasitism on host fishes. Based on the principles of optimal foraging (Werner 1977; Pyke 1979), we propose a hypothesis addressed to the variation observed in indices of lamprey feeding activity: wounding, scarring, and host mortality plus the growth rates of lamprey and host fishes.

As outlined by Applegate (1950) sea lampreys (*Petromyzon marinus*) spend a variable period of years as ammocoetes, transform to the parasitic stage

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TABLE 1. Symbols and parameter values used for simulating lamprey growth.

Symbol	Parameter description	Parameter value	Source[a]
a_1	Coefficient for maximum consumption	$0.30\ g \cdot g^{-1} \cdot d^{-1}$	2, 3
b_1	Exponent for maximum consumption	-0.35	2, 3
$T_{0,c}$	Optimum temperature for consumption	18°C	3
$T_{m,c}$	Maximum temperature for consumption	25°C	3
Q_c	Slope for temperature dependence of consumption	2.3	4
a_2	Coefficient for maximum standard respiration	$0.0105\ g \cdot g^{-1} \cdot d^{-1}$	1
b_2	Exponent for maximum standard respiration	-0.05	1
$T_{0,r}$	Optimum temperature for standard respiration	25°C	1
$T_{m,r}$	Maximum temperature for standard respiration	30°C	1
Q_r	Slope for temperature dependence of respiration	2.1	1
S	Specific dynamic action coefficient	0.15	4
A	Activity coefficient	1.5	
α_1	Coefficient for proportion of consumed food egested	0.03	2
α_2	Coefficient for proportion of consumed food excreted	0.15	2

[a]Parameter sources: 1, Beamish (1973); 2, Farmer et al. (1975); 3, Farmer et al. (1977); 4, Kitchell et al. (1977).

at about 5–10 g wet weight, and begin foraging. In 12–20 mo in the Laurentian Great Lakes (and as long as several years in marine waters), lampreys grow to adult sizes (>100 g) and make a terminal spawning migration. Size of returning adults is highly variable both within and between studied systems and may vary by as much as an order of magnitude (Johnson and Anderson 1980).

Variation in growth rates of individual lamprey reflects the interactions of parasitic or predatory activity and environmental conditions. Knowledge of the mechanistic controls for growth processes plus a known growth record and thermal history allow estimation of total food consumption. Seasonal patterns of food consumption may then be estimated to assess impact on the food resource and constraints imposed by the environment.

The Bioenergetics Model

The modeling approach used herein is similar to that described by Kitchell et al. (1977). This approach has been used successfully for various other applications including studies of polychlorinated biphenyl (PCB) uptake by lake trout (*Salvelinus namaycush*) (Weininger 1978), bioenergetic spectra of tunas (Kitchell et al. 1978), thermal effects on predator–prey systems (Kitchell 1979), the role of habitat in lentic predator–prey systems (Breck and Kitchell 1979), and the impact of Lake Michigan salmonids on their forage base (Stewart 1980). We will not attempt to detail the whole model-building process in this case, but describe the general principles and specific modifications made for applications to the lamprey.

The growth rate of an individual lamprey is calculated as daily weight change per unit of weight ($\Delta B/B\Delta t$) and is defined by the energy budget equation, with all units expressed as biomass equivalents:

(1) $\Delta B/B\Delta t = C - (R + F + U)$

where

$\Delta B/B\Delta t$ = specific rate of growth
C = specific rate of consumption
R = specific rate of respiration
F = specific rate of egestion
U = specific rate of excretion

Parameters for the model were derived from the literature on lamprey physiology and summarized (Table 1).

Specific consumption rate depends on weight, B, and temperature and is scaled as a proportion of the physiological maximum, $C_{\max}$, as follows:

(2) $C = C_{\max} P r_c$

where

$C_{\max} = a_1 B^{b_1}$; a_1 and b_1 are allometric coefficients
P = proportion of the maximum ration (0.0–1.0)
r_c = a temperature-dependent proportional adjustment (0.0–1.0) of maximum consumption rate at the optimum temperature. (See Kitchell et al. (1977) and Breck and Kitchell (1979) for details of this function.)

Total respiration rate is dependent on weight, temperature, activity, and ration level. As for consumption, the specific standard respiration rate, $R_{\max}$, is defined for a particular temperature (T_0, see Table 1), then modified by proportionality constants:

(3) $R = R_{\max} A r_R + SC$

where

$R_{\max} = a_2 B^{b_2}$; a_2 and b_2 are allometric coefficients
A = an activity parameter having values ≥ 1.0; we estimated the value as 1.5 for all applications to free-living lampreys

r_R = a temperature-dependent proportional adjustment (0.0–1.0) as for consumption

S = the specific dynamic action coefficient; i.e. the metabolic cost of ingestion, digestion, and assimilation expressed as a proportion of the ration

An important assumption made in developing parameters for equation 3 is that activity levels vary directly with the specified weight and temperature dependence of respiration. To our knowledge, there are no data available that would provide a better, empirical estimate of the value of A. The value of 1.5 was chosen to best fit data from Farmer et al. (1977) and remains an untested hypothesis. This assumption may have biased our estimates of consumption but, as specified, introduces an error on the order of $\pm 10\%$ in the total energy budgets calculated.

We assumed that blood is the primary food of parasitic lampreys; thus, values for egestion (F) and excretion (U) were taken as simple proportions of the ration (C). Although more complex functions of ration, body size and temperature may be developed (Elliott 1976), experimental data for lamprey are not fully available and the sum of waste losses appears to be a relatively constant proportion of ration (Kitchell et al. 1977).

Substitution of terms (S, F, and U) which are constant fractions of ration (Table 1) in equation (1) yields growth as the difference of rates of feeding and rates of energy loss:

$$(4) \quad \frac{\Delta B}{B \Delta t} = C_{\max} P r_c - (R_{\max}\, 1.5 r_R + 0.33C)$$

In other words, 67% of energy consumed is available for standard respiration, activity, and growth. As respiratory costs take energetic precedence, growth will vary as a function of P, the proportion of a maximum ration consumed. For a given ration, temperature, activity level, and body size, respiratory costs are fixed. Thus, the greatest variation will be expressed in rate of growth, the last demand satisfied in the sequence of energy budgeting processes.

Equations 1–4 and parameters in Table 1 describe the rules of energetics as applied to the sea lamprey. In effect, the equation series describes a null hypothesis which states that lamprey growth rates are primarily determined by temperature and body size effects. This complex set of relationships is distilled to a single free variable, P, when applied to a data set of known growth and thermal history for a specific lamprey population. By varying P to afford the best fit to the end points of a growth stanza (e.g. over a full year), the predicted growth may be compared with observed growth within the period. Substantial deviation of the model from observed data requires that the null hypothesis be rejected and that feeding rates and/or activity levels do vary independently from the assumed temperature and size dependence. Any independent measure of food availability and feeding rate or activity level would thus allow determination of the importance of each variable. To the best of our knowledge, no study has been conducted to date that made independent measures of all components of the energy budget for any free-living fish.

Values of P required to optimize the fit of growth records obtained for different lamprey populations (i.e. different prey and/or thermal histories) may be quantitatively compared as an indication of the intensity of lamprey predation. In an energetics context, the maximum and sustained minimum positive values of equation 4 describe the upper and lower bounds of the fundamental niche for sea lamprey (Kerr and Werner 1980). Values of P that best fit the observed growth thus represent an approximation of the realized niche. Assumptions made to derive P values are presented as testable hypotheses.

Applications described in the following section are representative of the range of conditions observed for lampreys in the various Great Lakes. The seasonal thermal regime in each of the Great Lakes was approximated by a sine function, using one-half cycle to describe the sequence of ice-free water temperatures. Midway between ice-out and ice-in, the sine function incrased to the maximum temperature during summer stratification (Bell 1980). We assumed a constant 2°C under the ice. Temperature parameters used for each lake are specified in Table 2.

Model Evaluation

To obtain a graphic representation of the energy budgeting process with respect to temperature, we simulated the growth of a 50 g sea lamprey at maximum rations ($P = 1.0$). The output (Fig. 1) is in weight equivalents and includes a correction for dif-

TABLE 2. Temperature parameters specifying the seasonal thermal regime in each of the Great Lakes. Parameters were from Bell (1980) and Boyce et al. (1977).

Lake	$T_{\min}$ (°C)	$T_{\max}$ (°C)	Ice-out (Julian day)	Ice-in (Julian day)
Superior	2	16	150	360
Huron, Georgian Bay	2	19	120	360
Michigan	2	22	120	360
Ontario	2	23	120	360

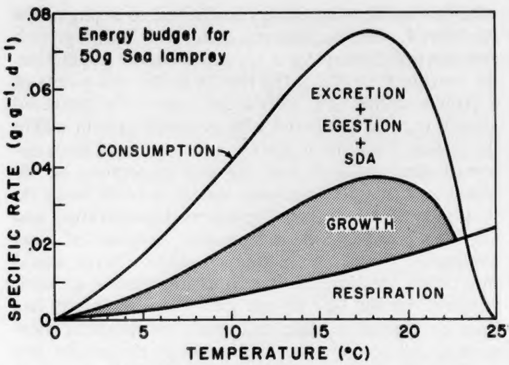

FIG. 1. Simulated energy budget for a 50-g sea lamprey as a function of maximum rations at all temperatures. Parameter values are from Table 1 and $P = 1.0$. Corrections were applied for energy differences between blood consumed and tissues stored as growth or used as metabolic substrates (see text).

ferences in energy density of host blood (3245 J/g or 765 cal/g wet weight) and that of lamprey tissue (5190 J/g or 1224 cal/g wet weight) (Farmer et al. 1975). Blood consumed has only 0.625 the energy density of the resultant biomass accumulated by lamprey as growth or respired in catabolic processes. As the model is based on biomass equivalents for lamprey weight, all rates of feeding calculated from observed lamprey growth were divided by 0.625 to estimate the weight of blood consumed.

To evaluate the simulation model, we compared its output with data from a laboratory study of the effects of temperature and weight on lamprey growth (Farmer et al. 1977). These data were derived by allowing lampreys to feed ad libitum on individual white suckers (*Catostomus commersoni*). If a host died, it was immediately replaced with a live fish. Although feeding was ad libitum, the nutritional quality of host blood declines quickly after attack by a lamprey (Farmer et al. 1975). Accordingly, average maximum rations expressed as energy intake would be expected to be less after the first day's feeding on any host and the resultant growth rate would yield a P value less than 1.0. We adjusted P to fit observed growth of a 50 g lamprey at 15°C ($P = 0.6$) and then compared simulated growth at that constant P for all observed weights and temperatures (Fig. 2). Observed data were derived from a multiple regression reported by Farmer et al. (1977) and have 95% confidence intervals of ±10–15% of the calculated values (G. J. Farmer Dep. Fisheries and Oceans, Halifax, N.S., personal communication).

The simulated growth rates of lampreys correspond very closely to those observed in the experiments. This is due, in part, to the fact that parameters for the maximum consumption terms in the model were derived from Farmer et al. (1977). Other components of the parameter table were independently derived (Table 1). More importantly, the data could be accurately simulated by manipulating only the value of P with the result that the model can effectively characterize lamprey growth over a range of temperatures and lamprey sizes simply by adjusting a single, biologically meaningful parameter, which is treated as an unknown.

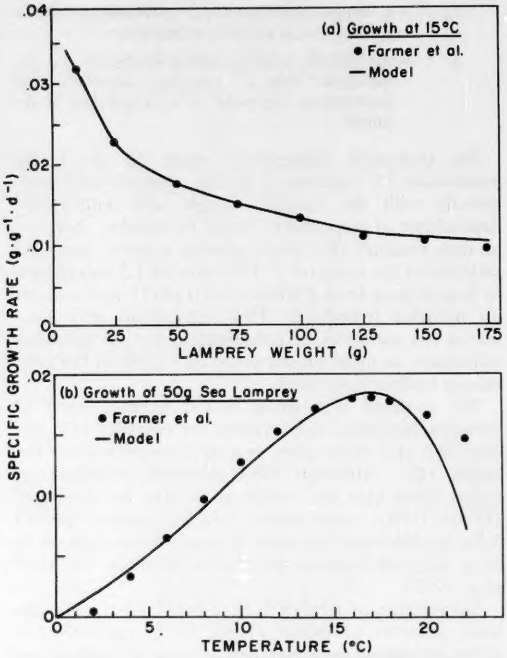

FIG. 2. Comparison of observed lamprey growth (Farmer et al. 1977) with growth simulated by the model. Parameters are given in Table 1 and $P = 0.6$. (a) Growth at 15°C for various lamprey sizes; (b) growth of a 50-g lamprey as a function of test temperature.

When applying this model to cases where the yearly increment in biomass is known, the model's predictions of total food consumed are quite insensitive to small changes in the physiological parameters. For example, if lamprey biomass increases from 10 to 286 g in one year in Lake Michigan, and the parameter P is used to fit this specified growth, then changes of ±10% in the most sensitive parameter (b_2, allometric exponent for respiration) yield changes of only ±1.0% in the predicted total food consumed. This relative insensitivity in predicted food consumption is due principally to using P to fit the observed initial and final biomass. This parameter is quite difficult to measure in the field and is least likely to be known, a justification for using it to fit the model to data.

A known growth record plus an estimate of thermal history thus allows a reasonably accurate estimate of

TABLE 3. Summary of simulated (Fig. 3–5) lamprey growth in selected Great Lakes applications. All simulations began with a 10-g lamprey on January 1 and were run for 1 yr.

Site	Source	Model estimates			
		Adult lamprey size (g)	P	Total consumed (g)	Gross efficiency (%) (ΔB/total cons.)
L. Ontario	Christie and Kolenosky (1980, Fig. 2)	156	0.45	520	28
N. L. Huron	Applegate (1950), J. Hunn, (U.S. Fish and Wildl. Serv., Hammond Bay, Mich.) personal communication	186	0.50	610	29
L. Michigan	Johnson and Anderson (1980, Fig. 3)	296	0.65	910	31
L. Superior	Johnson and Anderson (1980, Fig. 3)	215	0.65	630	33

the amount of food that must have been consumed during the growth interval.

Model Applications

GROWTH CURVES FOR GREAT LAKES LAMPREYS

Application of the model to lamprey in a specific system requires some knowledge of the primary host so that an estimate of thermal history can be developed. As examples, we chose data sets for lamprey associated with whitefish (*Coregonus clupeaformis*) in Lake Ontario and northern Lake Huron, and lake trout in Lake Michigan and Lake Superior. These data sets were selected because they represent a range of possible temperature conditions and different host species, and include intraseasonal estimates of lamprey growth derived from monitored fisheries.

In all cases, lamprey growth was simulated over an annual period beginning January 1. Initial weight was set at 10 g; final weights were estimated as the mean size of stream-run adults captured during December–January. A thermal history was constructed to reflect preferred temperatures of the prey type (Coutant and Carroll 1980). Where whitefish were primary hosts, maximum temperatures were set at 15°C during the period of summer thermal stratification (Coutant 1977 and references therein). For lake trout hosts, maximum summer temperatures were set at 12°C (Spigarelli 1975). For other periods, temperatures were assumed to be equivalent to surface water temperatures (Boyce et al. 1977).

Simulated weights were converted to lengths using a length–weight relationship derived from unpublished data provided by B. R. Smith (U.S. Fish Wildl. Serv., Marquette, Michigan, personal communication) total length (mm) $= 4.469$ (weight in grams)$^{0.304}$. Using these data and assumptions, P (Table 3) was adjusted so that the simulated growth would visually best fit the observed records (Fig. 3–5).

Each of the four growth curves derived from the model generally corresponds with the intraseasonal dynamics of observed growth. Where estimates of variability are available (L. Ontario and N.L. Huron), the simulated growth is regularly within one standard deviation of the monthly means (Fig. 3, 4). The November estimate of adult lamprey size in L. Ontario (Christie and Kolenosky 1980) is based on a sample size of 2 and the model, when fit to the larger data base of earlier samples, forecasts a mean adult size of 156 g. This is substantially smaller than the mean size of the two lampreys observed but comparable to the sizes of a large sample ($n = 1221$) of adult lampreys taken at the Humber River, Ontario in 1968 (Pearce et al. 1980).

As summarized in Table 3, estimated gross growth efficiencies (ΔB/Total Cons.) were similar in all four lakes, ranging from 28 to 33%. However, adult size

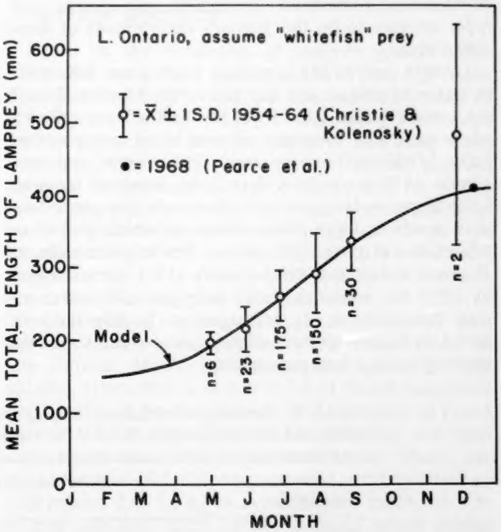

FIG. 3. Simulated and observed growth curves for lampreys in Lake Ontario. Observed growth data are from Christie and Kolenosky (1980) for lampreys removed from whitefish during 1954–64. Size of Humber River adults in 1968 is from Pearce et al. (1980).

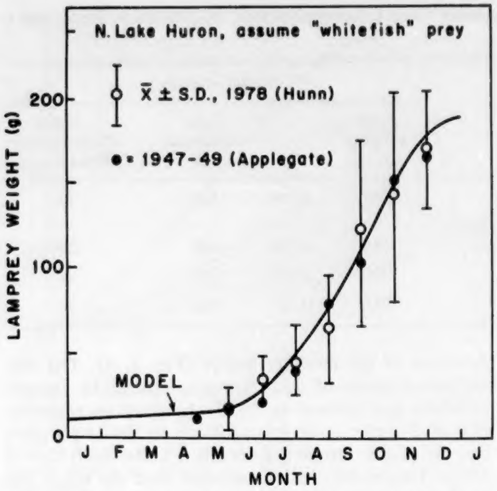

FIG. 4. Simulated and observed growth curves for lampreys in Northern Lake Huron. Observed growth data are from 1947 to 1949 (Applegate 1950) and 1978 (J. Hunn, U.S. Fish Wildl. Serv., Hammond Bay, Mich., personal communication) for lampreys collected primarily from whitefish fisheries.

and total food consumed differ between lakes. Thermal history, as dictated by differences in the heat budgets of lakes and midsummer association with specific prey type, appears to be the primary determinant of these differences.

Growth curves for lampreys feeding on lake trout in Lakes Michigan and Superior (Fig. 5) were fit with the same P value (0.65) yet resulted in very different adult sizes and estimates of total food consumption. Lake Michigan lamprey were 38% larger and consumed 44% more food than Lake Superior lamprey. Lake Superior lamprey consumed only 3% more food than northern Lake Huron lamprey, which preyed on whitefish, yet grew 20% larger. For a given value of P, lower midsummer temperatures (12°C for trout prey vs 15°C for whitefish prey) and generally lower annual temperatures (L. Michigan vs. L. Superior) resulted in highest growth efficiencies and the least relative impact on a host population.

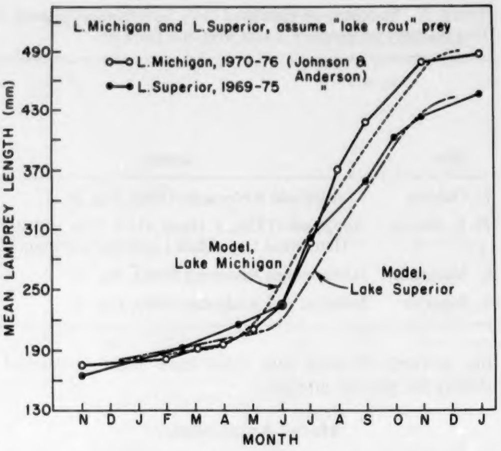

FIG. 5. Simulated and observed growth curves for lamprey in Lake Michigan and Lake Superior. Observed data are for 1970–76 (L. Michigan) ($n = 5284$) and 1969–75 (L. Superior) ($n = 2212$) from Fig. 3, Johnson and Anderson (1980).

THERMAL HISTORY AND HOST SPECIES

Based on the above results, we performed a series of simulations to evaluate the role of thermal history as dictated by association with a specific host in Lake Michigan. Three host types were considered: (1) a summer, epilimnetic resident (e.g. carp, *Cyprinus carpio*, or white suckers) that would experience temperatures up to 22°C, (2) a host (e.g. lake trout) that remains at the thermocline (12°C) during thermal stratification, and (3) a hypolimnetic host (e.g. chubs, *Coregonus* spp., or burbot, *Lota lota*) that would reside at maximum temperatures of 4°C. For each simulation we specified $P = 0.6$ in order to correspond with the experimental design and parameter values (Table 1; Fig. 2) of Farmer et al. (1977). Initial lamprey weight was 10 g and simulations were run for one year beginning on January 1. Results are summarized in Table 4.

Total food consumption, in this case, is directly related to maximum temperatures. In fact, consumption and growth rates decline for an epilimnetic resident

TABLE 4. Summary of simulated lamprey growth in Lake Michigan based on different host fishes and thermal histories. See text for explanation of assumed conditions.

Host habitat	Adult lamprey size (g)	Total consumed (g)	Gross efficiency (%) (ΔB/total cons.)
Epilimnion	234	920	24
Thermocline	247	810	29
Hypolimnion: Year I	53	125	34
Year I and II	138	400	32

during midsummer (see Fig. 1 and 2) when temperatures exceed 18°C, but the cumulative annual consumption is still greatest for this epilimnetic host type. As reported by Kitchell et al. (1977), growth rates were bimodal with late spring and early autumn maxima. Bimodal lamprey growth rates, as predicted here, are seen in data reported by Johnson (1969, Fig. 5) for lamprey taken from "coarse" fish, i.e. nearshore, surface-water fisheries in Lake Ontario. Lamprey growth apparently ceased during the midsummer period.

Lampreys feeding on thermocline residents had the greatest total growth. Due to the thermoregulatory behavior of the host, these lampreys showed no reduction in growth during midsummer.

Lampreys feeding on hypolimnetic hosts had highest gross growth efficiencies but had low feeding and growth rates. Although minimum and average sizes recorded for spawning adult lampreys are highly variable in the Great Lakes, fish smaller than about 100 g are probably not sexually mature. Thus, lamprey cannot attain sexual maturity in a single year of hypolimnetic residence unless able to feed at greater rates than specified by our simulations ($P = 0.6$) and/or the conditions of Farmer et al.'s (1977) experimental design. We continued the simulation for a second year (Table 4), which resulted in an average size sufficiently large for maturation by the late autumn spawning run. This prediction of a bioenergetics limit to life history processes corresponds with Applegate's (1950) assessment that maturation occurs after 12–20 mo in the parasitic phase.

Estimates of mortality caused by lamprey are variable. If lampreys functioned strictly as parasites, their impact would be seen primarily in reduced growth rate of host species and mortality would be very low. Changes in growth rates of L. Ontario salmon observed before and after development of a lamprey control program (Christie and Kolenosky 1980; Pearce et al. 1980) are good examples of the parasitic effect: growth rates of chinook (*Oncorhynchus tshawytscha*) and coho salmon (*O. kisutch*) more than doubled while the frequency of lamprey attack declined as a result of the control program; 90% reduction of the lamprey population corresponded with an order of magnitude reduction in scarring and wounding rates.

On the other hand, maximum mortality for a given amount of total blood consumption would occur if each lamprey attack were fatal after a minimum blood loss by the host fish. According to the regression equation developed by Farmer et al. (1975), the shortest time and the least blood consumed before host death both occur at the greatest blood loss rates. One way to estimate the largest biomass of fish killed would be to assume that each host is killed in only 1 d which G. J. Farmer (Dep. Fisheries and Oceans, Halifax, N.S., personal communication) periodically recorded during his studies of lamprey feeding behavior (Farmer 1980).

Then, according to the regression equation, each fish would die when it had lost 4.41% of its wet weight. Thus, one estimate of maximum mortality at highest total feeding rates would be (920/0.0441) = 20.8 kg of fish killed per lamprey per year in epilimnetic waters of L. Michigan. Actual mortality levels will be within these limits and will vary with the ratio of host:parasite sizes (Lett et al. 1975), thermal effects on feeding and growth rates, and foraging behavior of the lamprey.

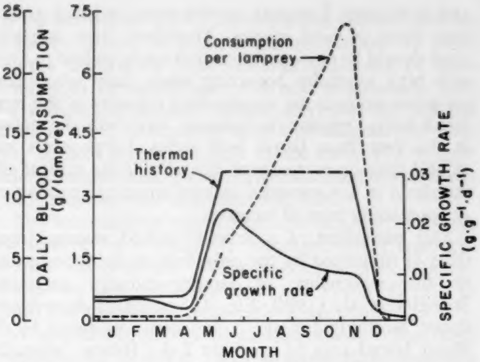

FIG. 6. Seasonal patterns of rates of feeding and growth for Lake Michigan lamprey associated with a host that resides at the thermocline (12°C) during thermal stratification.

SEASONAL PATTERNS OF LAMPREY GROWTH AND HOST MORTALITY

Based on the simulation of lamprey growth when associated with the lake trout-like prey in Lake Michigan and for $P = 0.6$, we estimated daily rates of growth and feeding (Fig. 6). Specific growth rates (grams per gram of lamprey per day) and daily blood consumption per lamprey have very different seasonal patterns. Growth rates increased rapidly with increasing water temperatures during April and May, peaking at about 2.3% per day, declined through the summer as the allometric effects on consumption rate occur, and declined even more rapidly with fall water temperatures. However, daily blood consumption per lamprey increases almost regularly throughout spring–fall then declines rapidly with dropping water temperatures in late autumn. Maximum consumption occurs in early autumn (Oct.–Nov.) at 6.0–7.5 g of blood consumed per day. Using Farmer et al.'s (1975) estimate of blood volume (% of fish weight) and maximum non-fatal daily blood loss (10% of the total blood volume per day) then [6.0–7.5 g blood consumed per day/(0.03 × 0.1)] yields 2.0–2.5 kg as the estimated minimum size of host fish that might survive lamprey attack during this period of rapid feeding by large lamprey.

Mortality of host fishes should thus parallel the rates of consumption per lamprey as dictated by seasonal temperature patterns and the relative size of lampreys and their hosts. Lamprey growth rates are much greater than those of host species. Therefore, host mortality rates should be size-specific and strongly pulsed in time, with high mortality occurring when daily blood consumption exceeds the regenerative capacity of the host. Small hosts, relative to lamprey size, will die earlier in the year than larger host fishes. Large hosts will exhibit little or no seasonal mortality if the critical size threshold is not exceeded before autumnal cooling reduces feeding rates of lamprey.

Our prediction of a strongly pulsed seasonal mortality is supported by the only field study done to date of the seasonality of lamprey-induced mortality. Spangler et al. (1980, Fig. 1) estimated lamprey-induced mortality for age 3 and older whitefish in the Burnt Island area of northern Lake Huron. Mortality was low until mid-August, increased seven-fold by Sept.–Oct., then declined equally rapidly by late November. Adult whitefish of this age and population are generally smaller than the critical minimum size described above. As expected from the prediction, mortality occurred in 92% of the estimated attacks.

The Foraging Hypothesis

Host mortality rates and wounding and scarring frequencies generally change as lamprey density varies. Within-system dynamics are reasonably consistent but the differences between host populations and between systems are remarkable. For example, lamprey-induced mortality is substantial when wounding and scarring frequencies are as low as a few percent of a total sample (Smith et al. 1974), yet some host populations persist when virtually all fish bear multiple scars (Pearce et al. 1980).

Studies summarized by Farmer (1980) indicate that a single feeding adult lamprey can kill even the largest of Great Lakes salmonids in a relatively short period. Many data presented in this symposium volume document that lamprey attacks are not inevitably fatal and that wounding or scarring rates may be very high with little evidence of correlative mortality (Pearce et al. 1980). Others demonstrate that mortality is highly correlated with lamprey abundance and wounding rates. Still others indicate that mortality correlates with indices of lamprey abundance but that wounding rates are low. As stated by Lett et al. (1975), the problem remains enigmatic.

The concept of an optimal foraging behavior by sea lampreys may serve to explain at least some of the conflicting observations on wound and/or scar frequencies relative to survival of the attacked fishes. The principles of optimal foraging have various origins and have been recently summarized in a series of applications to fishes (Werner 1977; Pyke 1979). The basis for application to the sea lamprey is summarized in Farmer (1980). A central assumption is that the lamprey is a facultative parasite, adapted primarily for feeding on blood but may act as a predator when food resources are limited. To demonstrate this concept, two important variables must be considered and may be expressed as ratios: the relative weights of host and lamprey; and the relative abundance of potential hosts per lamprey.

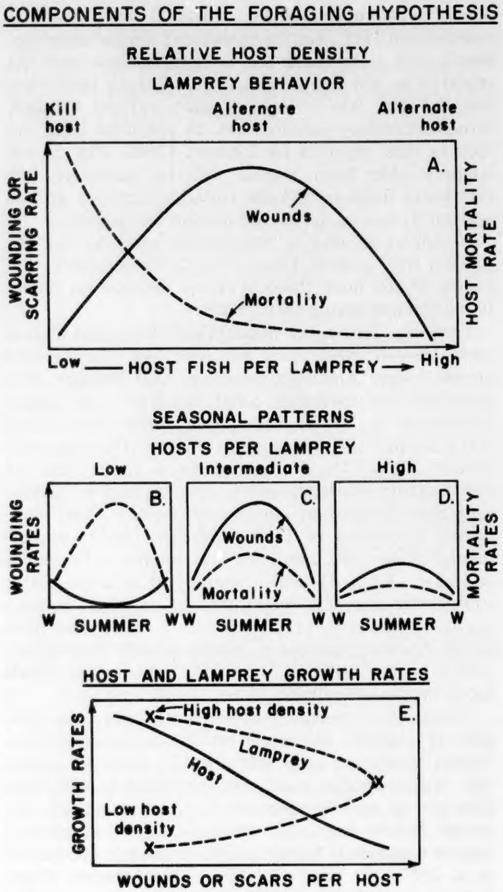
COMPONENTS OF THE FORAGING HYPOTHESIS
RELATIVE HOST DENSITY
LAMPREY BEHAVIOR
Kill host
Alternate host
Alternate host
A.
WOUNDING OR SCARRING RATE
HOST MORTALITY RATE
Wounds
Mortality
Low
HOST FISH PER LAMPREY
High
SEASONAL PATTERNS
HOSTS PER LAMPREY
Low
Intermediate
High
B.
C.
D.
WOUNDING RATES
MORTALITY RATES
Wounds
Mortality
W
SUMMER
W
W
SUMMER
W
W
SUMMER
W
HOST AND LAMPREY GROWTH RATES
E.
GROWTH RATES
High host density
Lamprey
Host
Low host density
X
X
X
WOUNDS OR SCARS PER HOST

FIG. 7. Proposed relationships between wounding, scarring, and mortality rates of host fishes and the relative abundances of lamprey and hosts (Panel A). Seasonal patterns are proposed for low (Panel B), intermediate (Panel C), and high (Panel D) ratios of hosts per lamprey. Growth rates of lamprey and host fishes are related to wounding rates and host density (Panel E). See text for assumptions made in developing these hypotheses.

As summarized in Fig. 7A, we hypothesize that this variable relationship may be explained, in part, by assuming that lampreys forage in an optimal way based on their perception of resource availability. To evaluate the role of variable fish density per lamprey, we assume that the weight ratio of fish:lamprey is constant and at a level that could result in death of the host. Density ratios will thus vary with population densities and, to a lesser extent, with short-term aggregating mechanisms much as midsummer thermal preferenda and/or seasonal spawning aggregations.

The key element of this hypothesis is that the lamprey perceives relative host density and exercises choice between acting as a parasite and as a predator. Selection should favor the former as blood is a rapidly renewable resource. There is evidence that fishes can appropriately modify their foraging behavior in response to changes in resource availability (Murdoch et al. 1975; Werner and Hall 1979).

When encounter frequency, expressed as host density, is low then the best strategy is to remain attached to one host exploiting its blood resource until it dies. As a consequence, wounding rates will appear low because few fish will survive the first lamprey attack and appear in an assessment fishery (Fig. 7A). Lamprey growth rates should be low due to reduced average quality of host blood resources and the lengthy interval between host encounters. Within a given system, host growth rates should be relatively rapid, reflecting the low density of host populations (Fig. 7E). High summer temperatures increase lamprey feeding rates and decrease resistance of a host fish to the stress of oxygen deprivation that results from rapid blood loss. Mortality and wounding rates should thus have reciprocal seasonal patterns (Fig. 7B). Asa Wright (Mich. Dep. Nat. Res., Okemos, Mich., personal communication) and A. Lawrie (Ont. Min. Nat. Res., Maple, Ont., personal communication) report that seasonal wounding patterns in Lake Superior lake trout exhibit summer minima. Among the Great Lakes today, Lake Superior probably has the lowest effective host density due to its relatively low productivity and substantial lamprey population. Accordingly, mortality per attack should be high and wounding frequency should be lower than in other systems.

Above some threshold host density which we consider intermediate (Fig. 7A, C), the optimum strategy for a lamprey would be to exploit the blood resource of a host until its quality declines (Farmer 1980), then move to an alternate host before the initial host dies. Thus, the resource is renewed as the initial host recovers and search time is minimal. Although some lamprey-induced mortality would occur, the rate per attack should be low and wounding rates observed in the fisheries should be high — in fact, highest (Fig. 7A). Corollaries should be seen in reduced growth rates of fishes with multiple wounds and scars (Fig. 7E) and increased lamprey growth. Wounding rates should have a strong summer maximum due to high lamprey feeding rates. These conditions appear in Christie and Kolenosky's (1980) study of whitefish in Lake Ontario: growth rates were inversely related to lamprey attacks and wounding rates had midsummer maxima.

Another example taken from Lake Ontario represents the descending, right hand limb of the foraging curve (Fig. 7A). Pearce et al. (1980) and Jolliff (1977) report very high wounding rates (averages of 10–13 per fish in 1971) for coho and chinook salmon in Lake Ontario. If, prior to the introduction of salmon, the lamprey in Lake Ontario had come to some steady-state or equilibrium with host populations, then the addition of stocked salmon increased the fish per lamprey ratio. As stocking rates increased and the lamprey control program began in the early 1970s, mortality rates declined, growth rates increased dramatically and wounding rates declined (Fig. 7D).

The last example comes from the Atlantic where the sea lamprey is a relatively inconspicuous component of fish communities. Wounding rates and lamprey abundance are low (Hardisty and Potter 1971). In effect, the fish per lamprey ratio is very high.

A second component of the hypothesis is that high wounding or scarring rates precede high mortality rates in time. As described in the preceding section, rapid growth rates of lamprey interact with temperature effects to yield a seasonal pulse of mortality. As lamprey size increases rapidly throughout the year, the minimum size of host fishes that will survive a single attack also increases rapidly. A trophic ontogeny effect will appear as pulses of mortality pass through the size spectrum of available hosts. If host species or cohorts are ranked by size, the seasonal progression should correspond with that ranking (Pyke et al. 1977) as modified by temperature effects and should generally follow the consumption per lamprey curve (Fig. 6).

We offer this hypothesis for critical evaluation. An analogue exists in the feeding behavior of predaceous, sucking insects; the length of time spent feeding on a prey decreased as prey density increased (Cook and Cockrell 1978). Although empirical relationships remain to be determined, the conceptual framework seems reasonable and may provide insights toward application of wounding and scarring rates to mortality patterns.

Any index of lamprey abundance should generally correspond with host mortality rates. However, the relationship is very probably not linear. The dynamics of lamprey feeding behavior, as represented by wounding and scarring rates, are a potentially more sensitive indicator of host–parasite interactions that precede the development of predator–prey dynamics. Thus, wounding and scarring rates should not be taken as simple correlates of mortality rates but as early manifestations of changing lamprey behavior that may ultimately be expressed in population dynamics. There exists an obvious need for additional experimental studies of lamprey feeding behavior which, because experimental work with sea lampreys is particularly difficult (Farmer 1980), may profitably be conducted by studying ecologically equivalent behavior of an analogous facultative parasite (i.e. other lamprey species). Similarly, carefully designed, controlled in situ manipulation of lamprey–host ratios may yield substantial benefit (Walters et al. 1980).

Acknowledgments

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Applegate, V. C. 1950. Natural history of the sea lamprey *Petromyzon marinus*, in Michigan. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. Ser. 55: 237 p.

Beamish, F. W. H. 1973. Oxygen consumption of adult *Petromyzon marinus* in relation to body weight and temperature. J. Fish. Res. Board Can. 30: 1367–1370.

Bell, G. L. 1980. NOAA Data Report ERL GLERL, Rep. No. 3, 4, 6, 7, and 8. Great Lake Env. Res. Lab., Ann Arbor, MI.

Boyce, F. M., W. J. Moody, and B. L. Killins. 1977. Heat content of Lake Ontario and estimates of overall surface heat fluxes during IFYGL. Inland Waters Directorate, Canada Centre for Inland Waters, Burlington, Ont. Tech. Bull. 101: 120 p.

Breck, J. E., and J. F. Kitchell. 1979. Effects of macrophyte harvesting on simulated predator–prey interactions, p. 211–228. *In* J. E. Breck, R. T. Prentki, and O. L. Loucks [ed.] Aquatic plants, lake management, and ecosystem consequences of lake harvesting. Proceedings of a conference at Madison, Wisconsin, February 14–16, 1979. Institute of Environmental Studies, University of Wisconsin-Madison, Madison, WI.

Christie, W. J., and D. P. Kolenosky. 1980. Parasitic phase of the sea lamprey (*Petromyzon marinus*) in Lake Ontario. Can. J. Fish. Aquat. Sci. 37: 2021–2038.

Cook, R. M., and B. J. Cockrell. 1978. Predator ingestion rate and its bearing on feeding time and the theory of optimal diets. J. Anim. Ecol. 47: 529–549.

Coutant, C. C. 1977. Compilation of temperature preference data. J. Fish. Res. Board Can. 34: 739–745.

Coutant, C. C., and D. S. Carroll. 1980. Temperatures occupied by ten ultrasonic-tagged striped bass in freshwater lakes. Trans. Am. Fish. Soc. 109: 195–202.

Elliott, J. M. 1976. Energy losses in the waste products of brown trout (*Salmo trutta*). J. Anim. Ecol. 45: 561–580.

Farmer, G. J. 1980. Biology and physiology of feeding in adult lampreys. Can. J. Fish. Aquat. Sci. 37: 1751–1761.

Farmer, G. J., F. W. H. Beamish, and P. F. Lett. 1977. Influence of water temperature on the growth rate of landlocked sea lamprey (*Petromyzon marinus*) and the associated rate of host mortality. J. Fish. Res. Board Can. 34: 1373–1378.

Farmer, G. J., F. W. H. Beamish, and G. A. Robinson. 1975. Food consumption of the adult landlocked sea lamprey, L. Comp. Biochem. Physiol. 50A: 753–757.

Hardisty, W. M., and I. C. Potter [ed.]. 1971. The biology of the lampreys, Vol. I. Academic Press, New York, N.Y. 423 p.

Johnson, B. G. H. 1969. Some statistics of the populations of parasitic phase sea lampreys in Canadian waters of the Great Lakes. Proc. Conf. Great Lakes Res. 12: 45–52.

Johnson, B. G. H., and W. C. Anderson. 1980. Predatory-phase sea lampreys (*Petromyzon marinus*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37: 2007–2020.

Jolliff, T. M. 1977. Sea lamprey studies in New York water of Lake Ontario. Rep. Great Lakes Fish. Comm. Attachment VI, Dec. 1977, p. 167–180.

Kerr, S. R., and E. E. Werner. 1980. Niche theory in fisheries ecology. Trans. Am. Fish. Soc. 109: 254–260.

Kitchell, J. F. 1979. In search of an optimal environment, p. 31–33. *In* R. Stroud and H. Clepper [ed.] Predator–prey systems in fisheries management. Sport Fishing Institute, Washington, D.C. 504 p.

Kitchell, J. F., W. H. Neill, A. E. Dizon, and J. J. Magnuson. 1978. Bioenergetic spectra of skipjack and yellowfish tunas, p. 357–368. *In* G. Sharp and A. E. Dizon [ed.] Physiological ecology of tunas. Academic Press, New York, NY.

Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34: 1922–1935.

Lett, P. F., F. W. H. Beamish, and G. J. Farmer. 1975. System simulation of predatory activities of sea lampreys, *Petromyzon marinus*, on lake trout, *Salvelinus namaycush*. J. Fish. Res. Board Can. 32: 623–631.

Murdoch, W. W., S. Avery, and M. E. B. Smyth. 1975. Switching in predatory fish. Ecology 56: 1094–1105.

Pearce, W. A., R. A. Bream, S. M. Dustin, and J. J. Tibbles. 1980. Sea lamprey (*Petromyzon marinus*) in the lower Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1802–1810.

Pyke, G. H. 1979. Optimal foraging in fish, p. 199–202. *In* R. Stroud and H. Clepper [ed.] Predator–prey systems in fisheries management. Sport Fishing Institute, Washington, D. C. 504 p.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. 52: 137–154.

Smith, B. R., J. J. Tibbles, and B. G. H. Johnson. 1974. Control of the sea lamprey (*Petromyzon marinus*) in Lake Superior, 1953–1970. Great Lakes Fish. Comm. Tech. Rep. 26: 60 p.

Spangler, G. R., D. S. Robson, and H. A. Regier. 1980. Estimates of lamprey-induced mortality in whitefish, *Coregonus clupeaformis*. Can. J. Fish. Aquat. Sci. 37: 2146–2150.

Spigarelli, S. A. 1975. Behavioral response of Lake Michigan fishes to a nuclear power plant discharge, p. 479–498. *In* Environmental effects of cooling systems, International Atomic Energy Agency (IAEA), Vienna.

Stewart, D. J. 1980. Salmonid predators and their forage base in Lake Michigan: A bioenergetic-modeling synthesis. Ph.D. thesis (Zoology), Univ. Wisconsin-Madison, Madison, WI. 225 p.

Walters, C. J., G. Spangler, W. J. Christie, P. J. Marion, and J. F. Kitchell. 1980. A synthesis of knowns, unknowns and policy recommendations from the Sea Lamprey International Synposium. Can. J. Fish. Aquat. Sci. 37: 2022–2208.

Weininger, D. 1978. Accumulation of PCBs by lake trout in Lake Michigan. Ph.D. thesis (Water Chemistry), Univ. Wisconsin-Madison, Madison, WI. 232 p.

Werner, E. E. 1977. Species packing and niche complementarity in three sunfishes. Am. Nat. 111: 553–578.

Werner, E. E., and D. J. Hall. 1979. Foraging efficiency and habitat switching in competing sunfishes. Ecology 60: 256–264.

Benefits and Costs of Sea Lamprey (*Petromyzon marinus*) Control in the Great Lakes: Some Preliminary Results[1]

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TALHELM, D. R., AND R. C. BISHOP. 1980. Benefits and costs of sea lamprey (*Petromyzon marinus*) control in the Great Lakes: some preliminary results. Can. J. Fish. Aquat. Sci. 37: 2169–2174.

While economic studies of the Great Lakes fisheries are still in their infancy, evidence is accumulating which suggests that efforts to rehabilitate the salmonid fisheries of the Great Lakes, including sea lamprey control, are paying rich dividends; benefits may exceed costs by half a billion dollars each year. Sportfishing values are much greater than commercial fishing values, so anglers benefit most from sea lamprey control. Expanding rehabilitation efforts in ways that will enhance angler success may also be economically sound. PCB levels in Great Lakes salmonids may be lowering the value of angling; 30% of anglers surveyed report eating less of their catch as a result of warnings. However, 93% oppose discontinuing stocking because of the PCB problem. The effects of possible energy shortages are difficult to predict, and may not necessarily reduce Great Lakes fisheries values.

Key words: sea lamprey, benefit–cost analysis, fishery economics, recreation economics

TALHELM, D. R., AND R. C. BISHOP. 1980. Benefits and costs of sea lamprey (*Petromyzon marinus*) control in the Great Lakes: some preliminary results. Can. J. Fish. Aquat. Sci. 37: 2169–2174.

Les études économiques des pêches des Grands Lacs peuvent être encore dans leur enfance, mais on a des indications de plus en plus nombreuses laissant penser que les efforts consacrés à la réhabilitation des pêches de salmonidés des Grands Lacs, y compris le contrôle de la grande lamproie marine, payent de riches dividendes; les bénéfices peuvent dépasser les coûts à raison d'un demi-milliard chaque année. La pêche sportive rapporte beaucoup plus que la pêche commerciale, de sorte que les pêcheurs à la ligne sont ceux qui bénéficient le plus du contrôle de la grande lamproie marine. Il peut être aussi économiquement sain d'intensifier les efforts de réhabilitation de façon à revaloriser la pêche à la ligne. Les niveaux de BPC dans les salmonidés des Grands Lacs peuvent diminuer la valeur de la pêche à la ligne; 30% des pêcheurs interrogés affirment manger moins de leurs prises par suite des mises en garde. Cependant, 93% s'opposent à l'arrêt des peuplements à cause du problème des BPC. Il est difficile de prédire les effets de la crise pétrolière, mais la valeur des pêches des Grands Lacs n'en sera peut-être pas nécessairement diminuée.

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SEA lamprey control is an expensive public enterprise, currently costing the United States and Canada about $5 million/yr. This leads to two kinds of economic questions. First, is the overall program, as presently implemented, worth the cost? In other words, are the benefits to the public greater than the costs for the program as it now stands? To answer this question economists may assess the "all-or-none values" of the program: a comparison of the public's economic well-being with the program as opposed to no program at all. Since we had no realistic way of separating the lamprey program from other rehabilitative and management efforts, such as fish stocking, management-oriented research, and law enforcement, in this paper we simply compared the all-or-none value of all Great Lakes fishing to total fisheries-related management expenditures. This assumes that management efforts are entirely responsible for the fishery; it overstates benefits to the extent that the fishery would generate some economic benefits at zero management expenditures.

The other kind of question is whether the level of funding for sea lamprey control is optimal. This requires a large amount of information about both the

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biology of the system — to be able to predict the results of alternative treatment and rehabilitative strategies — and the economics of sport and commercial fisheries — to be able to predict the changes in economic values caused by changes in fish populations. Economists refer to such changes in values and costs as "marginal values" and "marginal costs." Values of changes in sportfishing resources vary greatly from one location to the next and from one type of change in management strategies to another. Because of this and because the market price information economists usually rely upon for such values is absent, marginal values of sportfishing resources are particularly difficult to estimate and to generalize about. Simulation models capable of estimating many of these values for Great Lakes sportfisheries are just now becoming available, and marginal values reported in this paper are more tentative than the all-or-none values.

All-or-None Values

Basically, the economic value of anything, including the value of a fishery, is measured by what buyers are willing to pay for it. Value depends upon, (1) the tastes and preferences of potential buyers; (2) their ability to pay; (3) the particular goods being evaluated; and (4) the prices of possible substitutes. The same good can vary greatly in value, depending upon all these factors. The question associated with Great Lakes recreational and commercial fisheries is how much members of society would be willing to pay rather than do without the recreational opportunities and commercial fish products that the Great Lakes provide.

RECREATIONAL FISHERIES

Because recreational fishing is provided by the public sectors, market data are not available to estimate values for angling. However, anglers do pay the time and money costs associated with fishing, including costs for travel, fishing equipment, and possibly food and lodging. Anglers who travel farther generally incur greater costs, and we can observe that angling participation rates decline as costs increase. Based on such variations in participation rates, economists have developed a method to predict how anglers would respond to additional increases in costs; in other words, how much they would be willing to pay. These additional potential payments could, if necessary, be used to pay for the privilege of using the fishery resource, so that they represent the value of that resource.

To arrive at the values given below, various techniques were combined with this basic principle to estimate angling values for Michigan's Great Lakes. First, angling "quality" was identified. A total of 79 varieties of angling for Great Lakes fish in Michigan in 1976 were identified (C. S. Korson and D. R. Talhelm unpublished data; Korson 1979; S. W. Jordan and D. R. Talhelm unpublished data), based mainly on species groups, water-body type (Great Lake versus stream-run), season and angler success rates. Second, the demand for each of the 79 varieties was estimated. Each demand equation estimates angler preferences in terms of their willingness to pay for that kind of angling and their willingness to accept other similar kinds of angling as substitutes (C. S. Korson and D. R. Talhelm unpublished data; Korson 1979). Finally a simulation model was constructed, including (1) the demand equations; (2) an inventory of the counties in which each kind of angling is found; and (3) information about county population, income per capita, and estimated costs of angling. The methodology and theory are described in D. R. Talhelm (unpublished data), are very similar to the methodology and theory described in Talhelm (1971, 1972, 1973a, b, c and 1978) and D. R. Talhelm and P. V. Ellefson (unpublished data).

One value estimated by the simulation model is the all-or-none value of sportfishing for Great Lakes fish in Michigan. We assumed, (1) that inland angling for non-Great Lakes fish would remain available and unchanged; (2) that fishing opportunities outside of Michigan need not enter the equations; and (3) that the prices of all kinds of angling for Great Lakes fish would rise simultaneously. Because cross-price coefficients could not be constrained to be equal, consumer surplus was calculated by raising all prices by a small increment, calculating the quantity demanded for each product for each origin, and summing the quantities times their respective price increments. This was repeated for each product for each origin until the estimated quantity was zero or less or until the estimated quantity began increasing (i.e. the demand curve either reached an inflection point and became positive or the substitution effect outweighed the price effect).

We estimated that under these assumptions the all-or-none value was $102 million for 6.2 million angler days fishing for Great Lakes fish in Michigan by Michigan residents in 1976. This is an average of about $21/d in 1979 dollars (i.e. after allowing for inflation between 1976 and 1979 as measured by the Consumer Price Index), and is very similar to earlier projections by Talhelm (1979) based upon a similar study of anglers who fished for Great Lakes salmon and steelhead in Michigan in 1970. A similar value per day also resulted from application of the same technique to Wisconsin Lake Michigan angling (Samples 1980). Assuming that $21/d holds for the entire Great Lakes, and expanding these figures to include non-Michigan residents who fished in Michigan as well as all other angling for Great Lakes fish, total all-or-none value is an estimated $537 million/yr, plus or minus about $200 million. This estimate is based upon an estimate by Talhelm et al. (1979) of 16–32 million angler days in 1979. In other words, anglers would, if necessary, pay a maximum conceivable amount of about $537 million/yr ((in addition to their estimated

$440 million actual annual angling expenditures (Talhelm et al. 1979)) to retain access to the Great Lakes fisheries in their present state rather than not have access at all.

COMMERCIAL FISHERIES

The all-or-none value of commercial fishing was estimated at about $12 million/yr (between $7 and $18 million), based upon a study by Ghanbari (1977) of the dockside demand and supply of lake whitefish and lake trout in the U.S. and of the bioeconomics of lake whitefish production in Michigan waters of Green Bay. The demand and supply model was a two-stage least squares analysis of the simultaneous U.S. demand and supply for the two species for the period 1960–73. The ratio of 1973 whitefish consumer surplus to 1973 whitefish landed value was about 0.22, and the ratio of 1973 whitefish producer surplus to 1973 landed value was 0.27. The bioeconomic model consisted of a surplus production model estimate of the whitefish yield and fishing effort relationship for statistical district MM1, including a factor for sea lamprey predation, and a linear cost of fishing effort relationship based upon Pattinson and Talhelm (1978). The model estimated that fishing effort since 1971 has been near the point of intersection of the cost curve and the sustained yield curve, and that about the same level of yield could be produced at half the effort and cost. Since this district produced about 20% of the total U.S. production of whitefish in the mid-1970s, the bioeconomic model of Green Bay seems to confirm the U.S. producer surplus values estimated through the demand and supply analysis.

Ghanbari (1977) combined these results and found that the all-or-none value of the whitefish resource to producers and consumers (i.e. the maximum conceivable willingness of consumers and producers to pay for access to the resource, not including present market costs to consumers or production costs to producers) was around half as much as the current dockside revenue. Assuming this ratio holds for all commercially caught fish from the Great Lakes, and knowing that the reported dockside (landed) value in 1978 was about U.S. $23 million, our all-or-none value estimate was about U.S. $12 million in 1979 (Talhelm et al. 1979).

LAMPREY CONTROL

Sea lamprey control currently costs about $5 million/yr. Another $35–$45 million are spent for all other management and administrative activities related directly to Great Lakes fisheries. Some $12–$18 million of this total are paid directly by anglers and commercial fishers in the form of license fees, and the remainder comes from federal excise taxes on fishing equipment and general tax funds (Talhelm et al. 1979). The $12–$18 million paid by anglers and commercial fishers is considered part of the cost of fishing, not part of the all-or-none value of the fisheries. Attributing the full annual all-or-none value of the sport and commercial fisheries of roughly $550 million to the management program and setting the cost of the program at roughly $40 million annually yields a benefit–cost ratio of 15:1.

A pair of caveats are in order at this point. First, it is to be emphasized that economic analysis as applied to Great Lakes fishing is still in its infancy. Our estimates of both recreational and commercial values are based on extrapolations of Michigan and Wisconsin results to the entire Great Lakes of both countries, and even the Michigan and Wisconsin results may be revised after further study. Secondly, as noted above, the benefit estimates given here attribute the entire all-or-none value of the fisheries to the management program. In fact, some unknown portion of the all-or-none value would exist even if there were no management. Thus, our benefits represent overestimates. However, particularly given the economic predominance of the recreational fisheries and the importance of salmon and trout to those fisheries, a very large share of the benefit-estimate can be linked directly to sea lamprey control and salmonid rehabilitation. While future research may change the numbers somewhat and improve understanding of what share of total all-or-none values to attribute to management, it is hard to imagine changes sufficient to alter the conclusion that the program of sea lamprey control, stocking, and management has been an outstanding economic success.

Economic Potential for Modifying the Program

Given that the program of fishery rehabilitation viewed as an all-or-none proposition is an economic success, the next question is whether changes in the program are feasible which would make its net benefits even larger. Such "fine tuning" could take a great many forms: increased or reduced levels of lamprey control; changes in stocking levels; changes in the mix of species stocked; changes in priorities for the locations of stocking and lamprey control; alterations in fisheries management; and the like.

The economic analysis of such changes is more complex than the analysis of all-or-none values, particularly on the recreation side. Neither the average expenditures of anglers (about $17/d, see Talhelm et al. 1979) nor average all-or-none values ($21/d, as discussed above) are adequate measures of the values associated with small changes in management strategies. Both expenditures and all-or-none values are averaged over all recreation days and over all locations whereas changes of the type to be considered here involve more modest increases or reductions in recreation days at specific locations. Modes of analysis specifically designed to deal with such marginal changes are necessary.

One approach involves simulation models of the type described above. To illustrate what happens, suppose

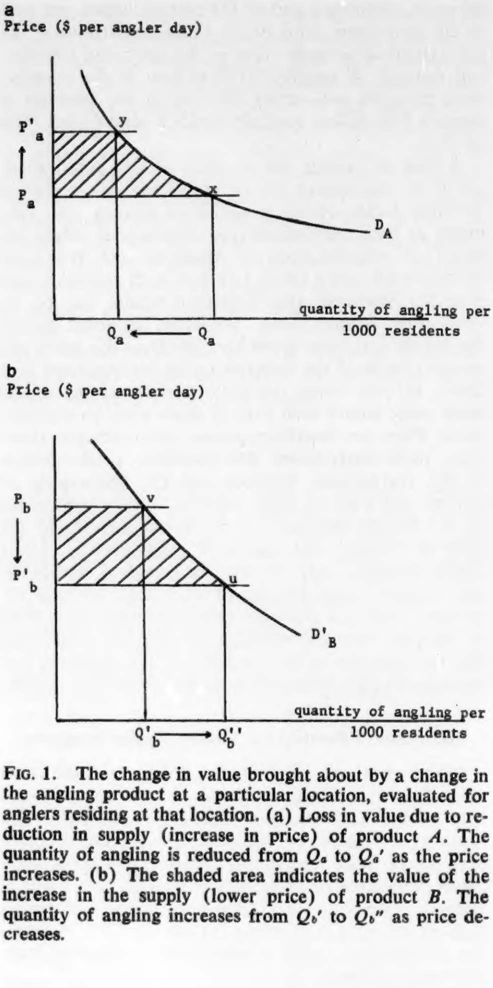

FIG. 1. The change in value brought about by a change in the angling product at a particular location, evaluated for anglers residing at that location. (a) Loss in value due to reduction in supply (increase in price) of product A. The quantity of angling is reduced from Q_a to Q_a' as the price increases. (b) The shaded area indicates the value of the increase in the supply (lower price) of product B. The quantity of angling increases from Q_b' to Q_b'' as price decreases.

that only two types of fishing exist. To keep the analysis simple, assume that the two types are not considered to be substitutes by the anglers. Let D_a and D_b in Fig. 1 be the demand curves for the two types of fishing for people in a given county. Let P_a and P_b represent the effective "prices" of the two fishing products for residents of the county in question. That is to say, these "prices" represent the costs per recreation day of participating in the two fisheries under current conditions. Now suppose that the particular site where residents of the county enjoy Type A fishing is converted to Type B fishing, perhaps by a stocking program. As a result, county residents are now able to enjoy Type B fishing at a lower "price" (i.e. cost), say P_b'. However, the site where they enjoyed Type A fishing no longer provides this service so that they must travel to a more expensive site involving a price (cost) of P_a'. Hence, the stocking program generates benefits (willingness to pay) equal to the shaded area P_b' uv P_b minus the shaded area P_a' xy P_a. It is entirely possible that this area could be negative, although Fig. 1 is drawn to show positive benefits. Within the simulation model, similar values for all other affected counties would be calculated and summed. The sum of all these benefits could then be compared with the costs of the stocking program to judge its economic feasibility.

This is basically how the simulation model for the Michigan Great Lakes waters functions, although it includes many more fishing products and allows explicitly for the fact that different types of fishing are often viewed as imperfect substitutes by consumers. To illustrate the results that might come out of the model in an actual application, suppose that all of Michigan's Lake Superior waters could be converted to a high success rate. This would mean a change in the product produced by each county since all currently provide either low or moderate success to anglers. How much would people be willing to pay for this improvement? The model predicts that the benefits would amount to about $75,000/yr and that the change would generate 70 000 additional angler days of recreation in Michigan's Lake Superior counties (a 40% increase).

A different approach to the question of how anglers would respond to improved success has been developed by Samples (1980). Data for his estimates comes from a survey of 750 Lake Michigan trout and salmon anglers completed in 1979. Over 85% of the sample returned the questionnaire. One approach to valuation applied in this study was to ask anglers how much they would be willing to pay for a special salmon and trout license for Lake Michigan if it would improve their average success by one fish per fisherman per day. Responses were analyzed using several variables and functional forms. The apparent best fit was attained with the equation ($R^2 = 0.48$):

$$\begin{aligned} \ln \mathrm{WTP} = -&\underset{(0.39717)}{0.9632} \ln \mathrm{ASR} + \underset{(0.12984)}{0.61624} \ln x_1 \\ &+ \underset{(0.10258)}{1.5966} \ln x_2 \end{aligned}$$

where

WTP = the willingness to pay of an angler for one additional fish per day.

ASR = the angler's current average success rate in fish per day.

x_1 = an index ranging from 1 to 4 of the angler's willingness to purchase special licenses, with 1 for least willing and 4 for most willing.

x_2 = an index ranging from 1 to 5 of the importance of fishing success to angler decisions about fishing sites with 1 being not very important and 5 being very important.

Numbers in parentheses represent standard errors of the respective estimates and show all variables to be significantly different than zero at the 0.025 level.

Taking the antilog of this expression and setting x_1 and x_2 at their mean values of 1.87 and 4.6, respectively, yield an expression of

$$\text{WTP} = \frac{16.835}{\text{ASR}^{0.9632}} \approx \frac{16}{\text{ASR}}$$

This equation may be thought of as the demand for increased success. As an angler's success rate increases, his/her WTP for additional success falls, as one might expect. Given the Wisconsin DNRs estimated success rate for the average angler of 0.4 fish/d, this equation implies that the average angler would be willing to pay \$40/yr to catch one additional fish per day. The survey indicated an average of 24 angler days per year so that the \$40 would average \$1.70/fish.

These results lead to cautious optimism about the potential economic returns from fishery management measures that would improve angler success. Other research at the University of Wisconsin suggests that such "hypothetical values" as our \$1.70 are substantial underestimates, and that a value of at least \$4 or \$5 would more closely approximate actual willingness to pay (Bishop and Heberlein 1979). Secondly, the figure of 24 d/yr is probably high. There is some evidence that people exaggerate the number of days they fish when responding to mail surveys. If so the value per fish would be still larger. For purposes of comparison it currently costs about \$1.60 per caught fish to stock salmonids in Lake Michigan, including about \$1/fish for propagation and distribution plus \$0.60 for capital costs. Judging by these figures, increased stocking could prove economically attractive provided the ecosystem is capable of supporting the fish.

Unfortunately, data problems necessitate caution in viewing these figures. Respondents to the survey reported an average success rate of 1.19 fish/d, far above the DNR estimate of 0.4 fish/d. If this ASR estimate is used in combination with 24 d/yr the value of an additional fish comes out to be only \$0.56. While the success rates reported on mail surveys are probably exaggerations, final judgement about the economic value of improved success must await further study.

Let us turn now from measures that improve fishing to adjustments that could adversely affect the fisheries. The potential for catastrophic declines in fish populations, which have been experienced in the past, received a great deal of attention from the SLIS modeling group. Important economic implications follow from this work. For example, under budgetary pressures which are probably inevitable, there may be a temptation to reduce the frequency of stream treatments or otherwise modify the lamprey control program. The modeling groups showed that reducing treatment levels below a threshold level could lead to such catastrophic fish losses. Should large reductions in salmonid populations occur, the all-or-none values (rather than the margin values) become relevant. At a total current cost of about \$5 million/yr, there is a danger that fine tuning of this kind might reduce costs by, say, \$1 million/yr while risking annual losses in recreational benefits of tens or even hundreds of millions of dollars. The potential for catastrophic losses means that such penny pinching efforts should be viewed with a great deal of skepticism.

Future Prospects for the Great Lakes Fisheries

Will the tremendous economic success of Great Lakes fisheries rehabilitation continue into the future? The location of the Lakes relative to major population centers in the U.S. and Canada assures the existence of large potential markets for recreational fishing and commercial fish products. As in any economic enterprise, however, there is always uncertainty.

One immediate concern is PCBs. While U.S. Food and Drug Administration regulations do not affect recreational fishing directly, levels of PCBs in sport fish above health standards applied to fish from commercial sources raise serious questions about the economic justification for continued stocking of salmonids and perhaps even sea lamprey control itself. However, to discontinue stocking and lamprey control is only one method of dealing with the PCB problem, and a very extreme approach at that.

An alternative would be to depend on the recreationists to avoid unsafe levels of ingestion. In Wisconsin, for example, each copy of the fishing regulations carries a warning for trout and salmon over 20 inches from Green Bay and Lake Michigan. In addition, information about how to prepare the fish to reduce the PCB content has been widely disseminated.

This approach is having a substantial impact. The 1978 Wisconsin Lake Michigan Angler Survey indicated that 30% of the sports fishers are eating less of their catches as a result of the warning and that 40% have modified how they prepare their fish (Samples 1980). These percentages are remarkably high given that relatively few anglers catch enough fish to be capable of eating fish once per week or more. When asked how often they eat Great Lakes fish, only 8% responded that they do so more than four times per month. Given that 93% of the anglers surveyed oppose discontinuation of stocking because of PCBs, perhaps the public can receive adequate protection through published warnings and information about preparation alone while continuing to enjoy Great Lakes fishing.

At this writing the U.S. Food and Drug Administration has formally proposed to lower the standard for commercially caught fish to $2\,\mu\mathrm{L}\cdot\mathrm{L}^{-1}$ PCB from its present level of $5\,\mu\mathrm{L}\cdot\mathrm{L}^{-1}$. If this measure is adopted it will have a significant adverse effect on commercial fishing benefits. For example, in Wisconsin some whitefish, particularly from Green Bay, and possibly some of the fish from the newly reopened cisco (chub) fishery may not meet this standard. Wisconsin's only fish meal plant, which utilized alewives, is already shut down because of PCBs, forcing fishermen to seek larger alternative markets. Further tightening of the standards may make fish meal production in Wisconsin a thing of the past. The sum total could be a reduction of 50% in Wisconsin's harvest measured in dollars. Hopefully though, the economic impact can be reduced through harvesting smaller fish, locating and closing fisheries where PCBs are particularly high and other management policies. Furthermore there is encouraging, though still inconclusive, evidence that PCB levels in Lake Michigan fish are declining. The problem may turn out to be shortlived.

In addition to PCBs, another cloud on the horizon relates to energy. Will shortages and high costs of gasoline greatly reduce the demand for Great Lakes recreational fisheries? The long-term effects that being on the "ragged edge" of gasoline supplies will have on the Great Lakes fisheries is anybody's guess at this time. Overly simplistic predictions should be avoided. While shortages and higher prices would lead economists to expect some reductions in *total* gasoline use, it does not follow that gasoline use for recreational fishing in the Great Lakes will decline. A scenario where recreationists substitute Great Lakes fishing for more distant alternative activities is equally plausible, particularly for those portions of the Lakes nearest to population centers in the two countries. Only time will tell for sure.

Turning to the longer run, a number of problems are conceivable. For example, TFM may someday prove to be environmentally unacceptable, or lamprey may come to tolerate it or to reproduce in the Lakes themselves. Recent success of fisheries rehabilitation efforts should provide considerable economic justification for research and management programs to attempt to anticipate and deal with such problems. Hopefully, future problems can be solved in ways that will allow the recreational and commercial fishermen and fish consumers of the U.S. and Canada to continue to enjoy the economic rewards which the Lakes are now providing.

Acknowledgments

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Bishop, R. C., and T. A. Heberlein. 1979. Measuring values of extra market goods: Are indirect measures biased? Am. J. Agric. Econ. 61(5): 926–930.

Ghanbari, M. R. 1977. Optimum allocation of a renewable resource: a bioeconomic model of the Great Lakes whitefish fishery. Ph.D. thesis, Michigan State Univ., Dep. Agricultural Economics, East Lansing, MI. 180 p.

Korson, C. S. 1979. Defining angling quality and estimating the demand for Michigan's 1976 Great Lakes salmonid and non-salmonid sport fisheries. M.S. thesis, Michigan State Univ., Dep. Fisheries and Wildlife, East Lansing, MI. 132 p.

Pattison, F., and D. R. Talhelm. 1978. Fisheries economics data (series). Michigan State Grant Program, Univ. Michigan, Ann Arbor, MI. MICHU-SG-78-102A through 102J.

Samples, K. C. 1980. An economic analysis of integrated fisheries management: the case of Lake Michigan alewife/salmonid fisheries. Ph.D. thesis, Univ. Wisconsin — Madison, Dep. Agricultural Economics, Madison, WI. 192 p.

Talhelm, D. R. 1971. Measurement of non-market resource values. Am. J. Agric. Econ. 53(5): 904.

1972. Analytical economics of outdoor recreation: a case study of the southern Appalachian trout fishery. Ph.D. thesis, North Carolina State Univ., Raleigh, NC. 308 p.

1973a. Defining and evaluating recreation quality. Trans. N. Am. Wildlife Natural Resources Conf. 38: 183–191.

1973b. Evaluation of the demands for the salmon and steelhead sport fishery of 1970 — a condensed report, p. 62–72. *In* Michigan's Great Lakes trout and salmon fishery (1969–72). Mich. Dep. Natural Resources, Lansing, MI, Fish. Manage. Rep. 5: 105 p.

1973c. Evaluation of the demands for the salmon and steelhead sport fishery of 1970. Mich. Dep. Natural Resources, Lansing, MI, Fish. Rep. 1977: 69 p.

1978. Evaluating angling quality and management benefits in the U.S., p. 265–282. *In* J. S. Alabaster [ed.] Recreational freshwater fisheries (Proceedings). Water Research Centre, Stevenage, Herts., England. 312 p.

1979. Fisheries: dollars and cents. Water Spectrum 11(1): 8–16.

Talhelm, D. R., R. C. Bishop, K. W. Cox, N. W. Smith, D. N. Steinnes, A. L. W. Tuomi. 1970. Current estimates of Great Lakes fisheries values: 1979 status report. Great Lakes Fishery Commission, Ann Arbor, MI. 18 p.

Sea Lamprey (*Petromyzon marinus*) Control — Where to From Here?
Report of the SLIS Control Theory Task Force[1,2]

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Sea lamprey (*Petromyzon marinus*) control with selective toxicants has reduced sea lamprey abundance in the Great Lakes to levels which permit survival of desirable fish species, but development of alternate and supplemental control methods is essential since chemicals cannot be used indefinitely. The Task Force addressed hypotheses which relate to regulation of sea lamprey numbers during different life history stages and why sea lampreys appear to affect fish stocks differently in various bodies of water. Examination of the information about the various factors that control sea lamprey abundance, both natural and man-made, permitted the Task Force to develop several hypotheses and to indicate areas where additional emphasis or research could produce new or supplementary control methods. Efforts to develop an integrated program of sea lamprey control should be accelerated by development of present promising areas as well as expansion in new directions. Sea lampreys when compared with teleosts exhibit many features of a prototype vertebrate and some unique specializations. Physiological, biochemical, or behavioral differences between lampreys and teleosts may be exploitable for developing control techniques specific to sea lampreys.

Key words: sea lamprey, Great Lakes, population control, barrier dams, integrated pest management, buffer species, physiology, teleosts

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Le contrôle de la grande lamproie marine à l'aide de toxiques sélectifs a réduit l'abondance de cette espèce dans les Grands Lacs à des niveaux permettant la survie d'espèces de poissons désirables, mais, comme les substances chimiques ne peuvent être utilisées indéfiniment, il est essentiel de mettre au point des méthodes de contrôle alternatives et supplémentaires. Le groupe de travail a examiné les hypothèses concernant le contrôle de l'abondance de la lamproie aux différents stades de son cycle biologique et s'est demandé pourquoi cette espèce semble affecter les stocks de poissons d'une manière différente dans différentes masses d'eau. L'examen de l'information sur les divers facteurs, tant naturels qu'artificiels, qui contrôlent l'abondance de la grande lamproie marine a permis au groupe de travail d'émettre plusieurs hypothèses et d'indiquer les domaines dans lesquels un effort ou une recherche accrus pour-

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[2] Chairman: H. A. Regier; members: J. L. Allen, R. J. Beamish, R. E. Beaver, J. E. Breck, S. M. Dustin, L. F. Erkkila, W. E. Gaylord, A. Gorbman, L. H. Hanson, J. W. Heinrich, D. B. Jester, Jr., D. P. Kolenosky, E. Kott, A. K. Lamsa, S. V. Lewis, F. P. Meyer, L. Olesen Larsen, H. A. Purvis, C. M. Rovainen, L. P. Schleen, S. H. Smith, B. L. Swanson, J. Teeter, T. Valtonen, and J. G. Weise.

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raient conduire à des méthodes de contrôle nouvelles ou supplémentaires. L'intensification du travail dans les domaines prometteurs aussi bien qu'une expansion dans de nouvelles directions devrait être accélérée par la mise au point d'un programme intégré de contrôle de la grande lamproie marine. Si on les compare aux téléostéens, les grandes lamproies marines exhibent plusieurs des caractéristiques d'un prototype de vertébré et certaines spécialisations uniques. On pourrait exploiter les différences physiologiques, biochimiques ou éthologiques entre les lamproies et les téléostéens afin de mettre au point des méthodes de contrôle spécifiques à la grande lamproie marine.

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THE current sea lamprey (*Petromyzon marinus*) control program using selective toxicants has been successful in reducing the abundance of Great Lakes sea lampreys to a level which permits the survival of desirable salmonid fish stocks (Lawrie and McCallum 1980; Wells 1980). However, it is essential to develop effective supplementary and alternative control techniques since control with toxicants cannot continue indefinitely. In the future, the petroleum-based toxicant may become unobtainable, social pressures may preclude its application, or lampreys may become less vulnerable through the development of resistance or altered habits. Extensive registration studies have demonstrated the toxicant's efficiency and relative safety (Meyer and Schnick 1980) but future regulations may result in the ban of its use.

The Control Theory Task Force was asked to address hypotheses which relate to regulation of lamprey numbers. Regulatory mechanisms can be classified as: (a) natural; (b) human-induced; and (c) integrated, which includes the fostering of natural control factors augmented by selected forms of control by human design. Natural regulatory factors would include intra- and inter-specific factors as well as ecosystemic factors — including impediments and aids to migration and dispersal.

The different life history phases of the sea lamprey occupy diverse niches and vary considerably in their vulnerability to various control factors. To understand the potential for regulating sea lamprey abundance, it was first necessary to review the origin of the problem and its basic biology in the Great Lakes and elsewhere. Then various regulatory hypotheses were assessed according to their validity and applicability. In the process, areas requiring further scientific investigation were identified.

Natural Controlling Factors

ORIGIN AND SPREAD OF SEA LAMPREYS THROUGHOUT THE GREAT LAKES

It is generally accepted that the sea lamprey was absent from the Great Lakes above Niagara Falls until early in the 20th century, but its origin in Lake Ontario is conjectural. Some consider it a landlocked race in Lake Ontario (Hubbs and Lagler 1947; Scott and Crossman 1973), but Aron and Smith (1971) present evidence that sea lampreys entered Lake Ontario via the Erie (Barge) Canal. The Canal was built by the State of New York in 1817–25 to link the Hudson River to Lake Erie, and with connections to Lake Ontario (Davies 1979). The first documented report of a sea lamprey in Lake Ontario was made by Fothergill in 1835 (Lark 1973). The question arises that if sea lampreys were present in Lake Ontario prior to that time, why were they of so little concern in the 18th and early 19th centuries? S. H. Smith (USFWS, Ann Arbor, Michigan, retired, personal communication) notes that (a) sea lampreys were not mentioned in descriptions of fish resources by early writers; (b) they would have been observed, even at low abundance where spawning runs were blocked by mill dams; and (c) that they would have been included as a food source by western Europeans who colonized the area (Gage 1928) just as they were utilized for food by residents of the northeast coast of the U.S. (Goode 1884). However, Aron and Smith (1971) believe that sea lampreys probably were contributing to fish declines in Lake Ontario by the 1880s.

Indications are that sea lampreys were absent from the Finger Lakes prior to canal construction. There is no evidence of sea lamprey presence in Seneca and Cayuga lakes until the late 1800s (Gage 1928); the Seneca and Cayuga lakes branches of the Erie Canal were completed in 1829 and the Susquehanna River–Seneca Lake branch in 1833 (Hubbs and Lagler 1947). The latter canal also may have been an access route. Sea lampreys have been found in the upper reaches of the Susquehanna River about 320 km from the mouth (Bigelow and Schroeder 1948).

The St. Lawrence River has been considered a possible source of sea lampreys for Lake Ontario, but the small maximum size observed in Lake Ontario indicates lack of recruitment of large anadromous sea lampreys (Christie and Kolenosky 1980). The St. Lawrence rapids may have provided a deterrent to immigration before the seaway was constructed, but it has been suggested that sea lampreys could bypass the St. Lawrence rapids by ascending the Ottawa River and descending to Lake Ontario through the Rideau Canal.

Other theories to explain the introduction of sea lampreys into the Great Lakes include releases of ammocoetes as bait fish, as "accidental" contaminants of elver shipments for stocking purposes in the 19th century, and release by ships of ballast water that may have contained adult lampreys.

The movement of fish from Lake Ontario into the Upper Great Lakes was blocked by Niagara Falls until the Welland Canal was completed in 1829 (Davies 1979). Nevertheless, sea lampreys were not reported in Lake Erie until 1921, Lake Huron in 1932, Lake Michigan in 1936, and Lake Superior in 1946 (Applegate 1950; Christie 1974). One possible reason for the slow advance of the sea lamprey is that Lake Erie presents an ecological impediment. Suitable spawning streams are limited (Pearce et al. 1980) and the warm waters of the central and western basins may interfere with upstream movement for a long period each year. A similar temperature blockage may exist in Lake Ontario's Bay of Quinte where Christie and Kolenosky (1980) observed insignificant wounding on lake whitefish (*Coregonus clupeaformis*) and other species sampled there despite potential spawning tributaries entering the Bay.

Pollution also provides a barrier to lamprey movements and reproduction as evidenced by the lack of lampreys in the Fox River system (Lake Michigan) and some tributaries to lakes Erie and Ontario. As pollution abatement measures continue to improve water quality, more lamprey habitat will be created and additional control will be needed. Water quality improvement in recent years in several Great Lakes tributaries has resulted in new populations of larval sea lampreys being established in several areas, for example, in the St. Louis River (Lake Superior) and Peshtigo River (Lake Michigan) (R. A. Braem, USFWS, Marquette, Michigan, personal communication).

Canals and blockages have a number of implications for sea lamprey control. The barrier dam program obviously is capitalizing on an effective means of limiting access to important lamprey spawning habitat, thus reducing the need for lampricides. Existing barriers should be maintained and new ones constructed where feasible. All proposals to remove dams or to renovate or build canals should be carefully scrutinized to ensure that sea lampreys are not allowed access to new spawning habitat or other watersheds. The Task Force suggests that the cost of a sea lamprey control program could be charged to transportation interests as a mitigation cost for shipping activities since shipping canals provided the route for invasion, certainly to the Upper Great Lakes.

The route(s) by which sea lampreys first invaded the Great Lakes, or the means by which they were introduced, is of some practical importance:

1) New invaders in appreciable numbers may continue to enter the Great Lakes by one or more of the routes used historically. Oneida Lake, part of the Erie (Barge) Canal, has large populations of larval sea lampreys in its tributaries and it has been demonstrated that there is downstream migration of transformed sea lampreys to Lake Ontario (Pearce et al. 1980). Any current incursions threaten the success of "integrated pest management" of the sea lamprey.

2) The Great Lakes watershed may contain two or more stocks of sea lampreys that diverged genetically through allopatric evolution. Thus, the Cayuga Lake population's genome may differ importantly from the genome of the Upper Great Lakes' stock, and may be a factor in the coexistence of sea lampreys and lake trout (*Salvelinus namaycush*) stocks in Cayuga Lake. Studies are underway to characterize genetically lamprey populations in the Great Lakes, certain Atlantic Coast drainages, and in the lakes of interior New York by means of biochemical (electrophoretic) markers. This information will give major insights into the population structure of the species and provide a sound basis for determining the origins of the freshwater populations. A better understanding of sea lamprey invasions will help to clear away confusion and improve the historic and scientific basis for managing Great Lakes resources.

From circumstantial evidence it appears that several decades at least were required to develop large sea lamprey populations following the introduction of a few adults into a lake. The evidence also suggests that at least a few adults could have travelled long distances into new areas of the Great Lakes system by hitchhiking on ships (Moore et al. 1974).

ADULT LIFE

Feeding habits — Following metamorphosis, sea lampreys descend Great Lakes streams over an extended time period beginning in late October and ending in early April (Applegate 1950). Purvis (1980) reports that mean lengths varied from 124 to 177 mm in the Great Lakes, but mean lengths above 160 mm were usually associated with reductions in population density of larvae resulting from lampricide treatment or limited recruitment. Metamorphosed animals are not usually observed feeding until they reach the lake although some feeding may occur in inland lakes or impoundments. Applegate (1950) and Johnson and Anderson (1980) observed no depth limitation to the distribution of feeding-phase sea lampreys, but rather an association with their prey. Recently metamorphosed lampreys appear in the deepwater areas of the Great Lakes where they have been captured by deepwater chub fisheries at depths greater than 79 m (Johnson and Anderson 1980). As the summer progresses, these animals move to the warmer, shallower waters ($\leq$40 m) (Applegate 1950). Laboratory studies on the relationship between lamprey feeding and growth suggest that lampreys feed in areas of the lakes where water temperatures range from 10 to 15°C during the summer and early fall (Farmer et al. 1977).

The Task Force believed that mortality is high during the period from transformation to the first feeding. They wondered by what mechanisms do some larvae successfully make this transition and others do not? Is the size (i.e. weight) at transformation the most important factor? Do downstream migrants in the fall have an advantage over spring migrants, or vice versa, or does this spread the risk in the event conditions in the lake are unfavorable? If migrants in the spring feed before entering one of the Great Lakes, greater productivity may be displayed by those systems having inland lakes. The Task Force felt that there is probably a higher and more variable mortality rate among recently transformed sea lampreys and small adults in the lake than among large adults. The smaller size of transformers and small adults makes them more vulnerable to predators than larger lampreys, but rapid growth (i.e. availability of food) can quickly reduce the number of potential predators large enough to prey on them. Therefore, low prey availability could lead to slower growth and increased mortality from predation among small lampreys. Further, small adults should be less able to withstand starvation than large adults. Transformers that wait until spring to migrate to the lake often have very low lipid reserves, so their mortality rate should be sensitive to prey availability. Perhaps the numbers of large feeding sea lampreys in the lake may be more dependent upon prey availability during the time they were small adults rather than on prey available when they are large lampreys. Reduced prey availability for large lampreys probably reduces lamprey biomass more than lamprey numbers.

Farmer and Beamish (1973) observed that sea lampreys given a choice of teleosts of different weights but of the same species select the largest individuals more frequently. Lampreys remained on trout until they had killed them in 54% of the cases, detached before feeding began in 37% of attacks, and detached after feeding but without killing their host in 9% of the encounters (Farmer et al. 1975). In the same study it was shown that lake trout mortality was directly related to the size of the lamprey. The larger the lamprey, the larger the lake trout must be to survive the attack. As lampreys grow over the summer, their impact on trout populations increases. Thus, wounding indices have been observed by many workers (Christie and Kolenosky 1980; Spangler and Collins 1980) to peak in late summer and early fall along with mortality rates. Heinrich et al. (1980) demonstrated that adult lamprey size was directly related to abundance of prey.

Many authors have discussed the devastating effect that the landlocked sea lampreys have had on the fish stocks of the Great Lakes. This impact is in contrast to the relatively benign activities of the anadromous *P. marinus* of the Atlantic Ocean, other parasitic lampreys found in various parts of the world (e.g. *Lampetra fluviatilis* and *L. ayersi*), and the landlocked sea lampreys in Oneida, Seneca, and Cayuga lakes, Lake Erie, and in Lake Ontario in the 1800s.

A difference in the manner of feeding has been noted in various lamprey species. *Lampetra fluviatilis* and *L. ayersi* actually consume a large portion of the muscle tissue as opposed to *P. marinus* which extracts the blood and body fluids. From an osmoregulatory point of view, a freshwater lamprey can utilize the additional salts of the blood while a saltwater lamprey would have to dispose of them. Conversely, the lower salt content of the muscle would reduce the problem of osmoregulation for the saltwater lamprey.

Both *L. fluviatilis* and *L. ayersi* feed primarily on lower trophic level animals which tend to be more abundant than the prey of *P. marinus*. The utilization of only the blood and body fluids of the prey is really a wasteful procedure since many kilograms of muscle tissue are effectively destroyed in the process if the host fish dies.

Effect on fisheries — Christie (1974) suggested two compatible hypotheses for the negligible impact of sea lampreys in Lake Ontario in the 1800s followed by a disastrous collapse of the lake trout and lake whitefish populations in the 1900s. The first relates to a minimal impact of lampreys when prey densities are high in relation to lamprey abundance (e.g. 1800s), whereas the second relates to the evolution of the lamprey as a parasite on large fish rather than a predator on small ones. Thus, the reduction in abundance and average size of fish in the stocks through commercial fishing invoked a predatory relationship. Lett et al. (1975) suggest a similar mechanism for the Cayuga Lake situation. Here, limited fishing mortality incurred by a sports fishery allows for the survival of older, larger trout which act as a buffer. This, coupled with varying lamprey recruitment are possible explanations for the coexistence of lake trout and sea lampreys.

For either of these hypotheses relating to size of prey to be functional, the abundance of lampreys must be limited to some degree by outside factors. In Christie's case, larval habitat was limited by mill dams blocking spawning streams during the 1800s. For Cayuga Lake, one tributary provides the major suitable larval habitat and the Lett et al. (1975) hypothesis included a requirement for varying lamprey recruitment. We would therefore like to suggest that the effect of a lamprey species on its prey populations increases as the ratio of prey abundance to larval habitat declines.

To support this relationship, we offer the observation that lamprey species exhibit a very high fecundity and are capable of maintaining a high production of ammocoetes with very low numbers of adult spawners. The limiting factor for lamprey production then would be stream or larval habitat and the impact of lamprey predation would be dependent on the amount of food available for the adults. In the ocean, food is virtually unlimited resulting in a high ratio of prey abundance to larval habitat. On the contrary, the Great Lakes exhibit a low ratio of prey abundance to larval habitat since larval habitat is extensive. The resulting production of adult sea lampreys is capable of outstripping the available supply of highly valued prey species, but does not collapse itself since alternate prey species such as suckers (catostomids) are capable of sustaining a viable lamprey population in the absence of its preferred prey.

There are exceptions to the standard disruptive sea lamprey response. A high ratio of prey abundance to larval habitat is found in Seneca Lake, Cayuga Lake, and Lake Erie, and in Lake Ontario during the 1800s; in these situations sea lampreys may not be a major source of mortality on fish stocks. On the other hand, Oneida Lake has considerable larval habitat, contains large populations of larval sea lampreys (Braem and Moore 1977), but provides less than optimum living conditions for adult sea lampreys since it is shallow, does not stratify, and the fishery consists of walleye (*Stizostedion vitreum vitreum*), yellow perch (*Perca flavescens*), and other warmwater species (Pearce et al. 1980). Pearce et al. (1980) believe that Oneida Lake is the most obvious source of sea lamprey recruitment to Lake Ontario and probably explains that lake's relatively large adult sea lamprey population in spite of control efforts. If a significant part of the sea lamprey population of Oneida Lake emigrates to Lake Ontario, we suggest that a small remnant population of adults in Oneida Lake would be sufficient to maintain the large larval populations in Oneida Lake tributaries.

If we examine the actual response of the prey species to lamprey attack, conflicting results are observed. First, Farmer (1980) indicates that a single feeding adult lamprey can quickly kill even the largest of Great Lakes salmonids in a relatively short period. However, SLIS authors have documented that lamprey attacks are not inevitably fatal and that wounding or scarring rates may be very high with little evidence of correlative mortality (Pearce et al. 1980; Youngs 1980). In opposition to these results are the observations by Spangler and Collins (1980), Lawrie and McCallum (1980), Budd and Fry (1960), and others that mortality is highly correlated with lamprey abundance and wounding rates. Still others indicate that mortality correlates with indices of lamprey abundance but that wounding rates are low (Kitchell and Breck 1980).

An optimal foraging hypothesis has been suggested by Kitchell and Breck (1980) to account for these discrepancies. The concept is based on two important variables, the relative weights of host and lamprey and the relative abundance of potential hosts per lamprey. The key element of the hypothesis is that the lamprey perceives relative host density and exercises choice between acting as a parasite or as a predator.

When host density is low, the lamprey continues feeding until the host dies. Consequently, wounding rates will be low and host mortality rates high. Above some threshold host density, the lamprey will continue feeding until blood quality declines, and then move to an alternate host before the initial host dies. Wounding rates will be high but mortality rates low. At still higher host densities, the fish to lamprey ratio is high and both wounding and mortality rates will be low. These different levels of wounding and mortality are associated with seasonal patterns of wounding and mortality of host species. Although Kitchell and Breck's (1980) optimum foraging hypothesis appears to offer insight into some reported patterns of fish mortality and sea lamprey wounding rates, it should be examined further to decide its validity, and if valid, determine the empirical relationships.

Spangler and Youngs (G. R. Spangler, University of Minnesota, St. Paul, Minnesota, and W. D. Youngs, Cornell University, Ithaca, New York, personal communication) hypothesized that rapidly growing host fish are more likely to succumb to the effects of a single lamprey attack than are slow-growing hosts. This suggests a mechanism whereby intensive exploitation may have "softened up" the Great Lakes fish community for catastrophic decline. The hypothesis is supported by (a) Christie and Kolenosky (1980), who demonstrated that growth increments in Lake Ontario whitefish were negatively correlated with the proportion of the stock wounded; (b) Spangler and Collins (1980), who found that the most rapidly growing stocks of Lake Huron whitefish were most affected by lamprey predation; (c) lamprey-induced mortality in lake whitefish was coincident with the period of maximum growth rate in northern Lake Huron (Spangler 1974); (d) Youngs' (1980) report of no significant lamprey-induced mortality in a slow-growing lake trout population in Cayuga Lake; and (e) observations that in Lake Superior lake trout growth is rapid and lamprey-induced mortality remains high (Lawrie and McCallum 1980).

There are a number of mechanisms which might account for the lethal effect on rapidly growing fish. Prey fish committed by hormonal regulation to a rapid growth regime may be unable to shunt their energy allocations into tissue replacement in time to prevent death. Alternatively, the host may be elaborating gonadal tissue prior to the onset of the fall spawning season. It may be relevant that spring spawning species, both native and exotic, were not extirpated during the fish stock declines in the Upper Lakes.

Lett et al. (1975) predicted through a simulation model that lake trout mortality increased geometrically with arithmetic increments in sea lamprey abundance. Farmer et al. (1975) suggested that a host-to-lamprey weight ratio of at least 40:1 allows host survival. They also reported on a host-to-lamprey weight ratio of 31:1 for Seneca Lake, New York, where sea lampreys and lake trout exist in equilibrium. By increasing the host to lamprey ratio, it should be possible to reduce lake trout mortality. This could be accomplished by increasing the number of lake trout stocked or by increasing the numbers of alternate prey or "buffer" species to relieve predation pressure. One problem that might be encountered in switching the predator to alternate prey is its apparent selection for lake trout where available. In addition, such a strategy could only be used in conjunction with a control program that would limit numbers of adult lampreys. Otherwise, the additional food provided to the lamprey could result in improved adult lamprey survival, and increased wounding. It is possible that hatchery-reared lake trout planted over remnant native lake trout stocks in Lake Superior may have been a buffer to the native lake trout stocks as the latter slowly increased in abundance.

The ultimate goal for fisheries managers should be to develop a stable fish community with a good cross section of species to utilize available habitat. To reach this balance, it may be necessary to provide a buffer for lake trout populations. If this is the case, it would appear that plantings of additional lake trout, lake whitefish, and salmon (*Oncorhynchus* spp.) could divert sea lamprey predation as part of an integrated control strategy aimed at maximizing lake trout survival and reproduction.

Spawning habits — During the summer and fall prior to spring spawning, sea lampreys begin to move inshore (Applegate 1950), and male lampreys appear to move inshore in advance of female lampreys while still feeding (Johnson and Anderson 1980). In addition to the inshore movement, there appears to be a period of sea lamprey dispersal. There was a general consensus among the Task Force that sea lampreys have none, or at best, a weak homing instinct, which promotes the continued invasion of new habitat. It is also believed that most lampreys probably do not disperse far from the area of their natal stream and will spawn in streams in the same general area. Nevertheless, some lampreys can travel hundreds of miles, often in short time periods, and have been known to move from one lake to another (Moore et al. 1974), a factor which would accelerate the continued invasion of new habitat. The mechanism for dispersal appears to be hitchhiking on boats and operates most strongly in the autumn. Divers using scuba gear examined hulls of 51 ships between June 26 and November 1, 1956, passing through the Canadian Sault Locks, but did not find the first lamprey until September 13 on the 36th ship examined. Fifteen ships examined subsequently yielded 11 lampreys (Great Lakes Fishery Commission 1956). No lampreys were observed in similar examinations of 44 ships between May 18 and September 14, 1957 (B. G. H. Johnson, Department of Fisheries and Oceans of Canada, Sault Ste. Marie, Ont., personal communication). In later trawling studies in the St. Marys River, sea lampreys attracted to a trawl boat (Dahl 1968) showed that activity generally began in September and peaked about mid-October to mid-November, with 90% of the lampreys being caught at temperatures between 4.4 and 10°C (A. K. Lamsa, unpublished data).

It also has been suggested that sea lampreys are "collected" by migrating schools of salmon which are homing to their planting sites. This may explain the accumulation of large numbers of sea lampreys in western Lake Ontario, in particular, the spawning runs into the Humber River which is blocked by dams with no spawning habitat available to lampreys (S. M. Dustin, Department of Fisheries and Oceans of Canada, Sault Ste. Marie, Ont., personal communication).

The lack of a strong homing instinct and ability to disperse suggests that sea lamprey control on a local basis would not be feasible and control efforts should be at least lake-wide if not Great Lakes basin-wide.

Sea lampreys require certain physical factors for successful spawning, including suitable gravel, satisfactory temperatures, and unidirectional water flow (Applegate 1950). It is believed that sea lampreys in the Great Lakes spawn in streams and rivers, and not in the lake because of the latter factor. The Task Force, however, discussed the possibility of lake spawning in areas where unidirectional water currents may occur. Water temperatures at many such locations may be too cold to initiate spawning or permit embryogenesis, but such areas should be identified and evaluated.

In 1971 and 1972 over a hundred spawning silver lampreys (*Ichthyomyzon unicuspis*) were observed by a scuba diver near the inlet to the St. Clair River in southern Lake Huron. In 1971 one spawning run sea lamprey was noted in association with silver lampreys (A. K. Lamsa, unpublished information; B. G. H. Johnson, Department of Fisheries and Oceans of Canada, Sault Ste. Marie, Ont., personal communication). Although sea lampreys were not specifically identified spawning in that particular area, the potential exists since the habitat investigated was small in comparison to that available in the St. Clair and Detroit rivers.

Sea lampreys spawn successfully in several areas of the St. Marys River (R. A. Braem, USFWS, Marquette, Michigan, personal communication), which is the outflow of Lake Superior. Spawning is delayed until midsummer, however, because of the slow rise in water temperatures in Lake Superior. These animals probably are a major cause of sea lamprey wounding and scarring observed in northern Lake Huron.

Stocks of lampreys that seem to be adapting to spawning in connecting water areas such as the St. Marys River pose long-term threats to control of sea lampreys since there is no practical methodology available for eradication. For example, any survival of St. Marys River sea lampreys to maturity and spawning may lead to an increasing population of animals that are genetically adapted to spawning in these and similar areas. Cold-water temperatures will slow growth and delay transformation, perhaps well beyond the normal 4 to 5 yr to transformation. As adults, they would drift downstream to feed on fish in the lower St. Marys River and northern Lake Huron. Since the St. Marys River is a major shipping channel, some of these sea lampreys would be carried back into the river hitchhiking on vessels and remain for spawning. Sea lampreys are caught in the fall in the St. Marys River as they try to attach to boats (Dahl 1968; Moore et al. 1974). Because of the long time between generations, it may take several decades for this type of population to develop into significant abundance. If the first sea lamprey began to spawn in the St. Marys River in the late 1930s or the 1940s, the attainment of a population adapted to spawning in the St. Marys River may not have become evident until in the late 1970s. Sea lamprey control personnel expressed the belief that the large population of sea lampreys in the St. Marys River may be increasing (R. A. Braem, USFWS, Marquette, Michigan, personal communication). The Canadian Sea Lamprey Control Centre reported in 1979 (J. J. Tibbles, Department of Fisheries and Oceans of Canada, Sault Ste. Marie, Ont., personal communication) that in one section of the St. Marys River the mean length of sea lamprey larvae decreased from 130 mm in 1963–64 to 90 mm in 1978. The percentage of larvae less than 100 mm increased from 9 to 69 during this period. A decline in mean length could indicate successful spawning and recruitment to the larval population in recent years compared with sporadic spawning and recruitment in earlier years. If this is true, the population could continue to increase unless measures are taken to reduce it — a difficult and expensive task with currently available techniques. On the other hand, because of the slower development of the larvae, control may only be needed once every one or two decades to reduce the "adapted" population. A lampricide treatment in the St. Marys River would be prohibitively expensive. Attractants and repellents, once they are developed, could be used to direct lampreys into suitable tributary streams for trapping, chemical eradication, or capture of males for sterilization and release in the river.

In the Great Lakes, spawning run sea lampreys appear in the rivers from late March through September, although most of the migration occurs in April to June (Applegate 1950; Manion and Hanson 1980). Generally the run begins as the water temperature rises above 4.4°C. Spawning takes place mostly in June and July, nest building begins at about 12°C, and peak spawning occurs at about 18°C (Manion and Hanson 1980). During the spawning run, and particularly during the spawning act, sea lampreys are probably vulnerable to greater predation by various animals than during their parasitic phase, but the overall effect on larval production is probably minor since spawning by a few adults can saturate the stream larval habitat.

Spawning run sea lampreys are attracted to potential spawning streams through several mechanisms. Physical factors such as river currents with desirable temperatures entering the lake or other attractants can draw lampreys upstream. Teeter (1980) reports that male sea lampreys that are sexually immature during the spawning season are attracted to waters with sea lamprey ammocoetes, but as they mature sexually, this attraction disappears. At a later stage of maturity, spawning lampreys are attracted by conspecifics of the opposite sex. The first (attraction by ammocoetes) may be important in guiding males into suitable streams, and the second (conspecifics) in bringing the spawning pairs together. Potential control of sea lampreys by use of pheremones to disrupt and confuse spawning animals is discussed by Teeter (1980) and Sawyer (1980).

The spawning act has been described by Applegate (1950) and Manion and Hanson (1980). Spawning is usually monogamous but can be polygamous. The male sex pheremone attracts females and repels males (Teeter 1980); the latter factor would tend to disperse the population over a wide area of habitat. If the spawning population is large, density-dependent intra-specific competition occurs through disruption of nests by subsequent and multiple spawning, but this is probably not significant in reducing overall hatching success. Further, the role of sex attractants would be more important when spawning animals are scarce than when they are abundant. A preponderance of females also is advantageous since one male can serve more than one female.

Interspecific factors also decrease spawning success. Insects, crayfish, and fish (minnows, sculpins, darters, and others) feed on eggs during the spawning act. Other predators may prey on the spawning lampreys or disrupt their spawning, especially since spawning sea lampreys become oblivious to external threats and can be approached easily, even in the daytime.

Density-independent factors may in some years cause considerable mortality of eggs and young larvae. Severe flooding can rearrange the stream bottom and destroy the nests, which may be particularly damaging late in the spawning period.

LARVAL LIFE

Life history — The fecundity of sea lampreys, larval production in nests, and influence of water temperatures on hatching success are discussed by Manion and Hanson (1980). Although the reported fecundity of female Great Lakes sea lampreys is high (average egg counts of about 56 000–69 000), the number of eggs actually deposited in the nest is much lower (average about 10 000). Survival of deposited eggs, however, is high (about 90%). Thus, despite the large egg loss during spawning, relatively few females can still produce a large number of larval sea lampreys.

The eggs hatch in about 2 wk; the hatched larvae emerge and pass downstream to burrow into silt beds in various parts of the river. This movement, which is not entirely passive, enables the animals to colonize favorable habitats. Factors such as water quality, temperature, and water flow affect larval dispersion in streams. Marking studies have also shown that ammocoetes already in suitable areas may remain there for up to 5 yr (Manion and McLain 1971).

Potter (1980) noted the wide variations in growth rates of ammocoetes in streams tributary to different Great Lakes, differences within some streams, and differences between sexes. Because habitat is heterogeneous with respect to growth potential for larvae, and because larvae tend to transform when they reach some threshold weight or length on the average (as opposed to transforming after some fixed time), the offspring of each year class will tend to transform over several years as has been shown to occur in the Big Garlic River study (Manion and Smith 1978). In addition, growth of reestablished lamprey populations following a lampricide treatment is generally faster than normal and slows as additional year-classes are established (Purvis 1979). Spreading the transformation of a year-class over several years reduces risk and increases the chances that some offspring will encounter acceptable conditions in the lake and the spawning stream. The risk reduction will be especially advantageous if the rate of survival of larvae tends to be higher than that of adults.

Information on migration of transformed sea lampreys to the lake is summarized by Potter (1980), who discusses the bimodal peaks (fall and spring) of sea lamprey movement, and notes that this enhances survival of the species by not exposing all the animals which transformed the same year to dangers at the same time.

In addition, the Task Force noted that the numbers of transforming lampreys migrating out of a stream during a given year apparently are unrelated to the size of spawning populations of any previous years, nor are they regulated by growth, sex ratio, and survival of feeding adults, or by prey abundance during the life of any previous year-class of predatory-phase lampreys. These observations reinforce the generally acknowledged plasticity of the animal and its capability to respond quickly to take advantage of changing conditions.

Competition — Who are the competitors? Which organisms share the limited resource? Competition for food or space may occur with ammocoetes of the same species, other species of lampreys, or other suspension feeders such as clams and mussels, and pool-dwelling, suspension-feeding insects.

Moore (1980) concluded that there is little information on the relative importance of various foods in the nutrition of ammocoetes. Earlier studies emphasized the large number of diatoms in the guts of various species, but there was no critical evaluation of the abundance of ingested algae. He suggests that the bacterial film associated with algae, detritus, and sand grains may be more important than previously suspected.

Food abundance varies spatially and by time of year in streams. Moore (1980) concludes that seasonal variations in intensity of feeding probably depend on temperature, whereas algal density and total amount of food available have little influence. The amount of food available in the stream may not be a significant factor in limiting ammocoete growth.

Food quality may be more important in limiting larval growth than food abundance. Some stream invertebrates and ammocoetes are known to prefer detritus colonized by bacteria and fungi to uncolonized detritus (Moore 1980). The detrital food quality decreases as the proportion of lignins, cellulose, and ash increases. However, little is known of effects of food quality on abundance of larval lampreys.

Is space a factor in limiting sea lamprey growth and abundance? There was Task Force discussion that some maximum biomass can grow in each habitat type, but the relationships were not clear. Because larvae are known to change locations when stressed, it suggests that availability of space in preferred (high quality) habitat occupied by increasing numbers of immigrants might be limiting growth of some ammocoetes already present, or stimulating further movement into other areas. Young-of-the-year sea lampreys appear to be found more in sand and gravel than silt–detritus habitat inhabited by older larvae, and will move to silt–detritus areas as they grow, adding to population pressures in those locations.

The Task Force discussed the mechanisms of competition, but no firm conclusions were reached. Was there a differential ability between lamprey species, or perhaps ammocoete sizes, to utilize the resource? Or were there behavioral interactions such as aggressive encounters, or excretion of inhibitory substances, including metabolites? Aggressive interactions between ammocoetes of different species (or within the same species) have apparently not been observed.

That control perhaps could be augmented by increasing interspecific competition during the larval stage through stocking of nonparasitic lampreys was discussed. Circumstantial evidence for competition among the several species of lampreys is provided by the generally limited overlapping ranges in streams (Morman 1979). Limited overlapping ranges, however, do not necessarily mean that competition is occurring now. Separation by differences in habitat preference may have reduced interspecific competition to negligible proportions. Sea lamprey ammocoetes inhabited a wide range of stream habitats (Morman 1979).

Predation — As previously noted, hatching rates of eggs in the nest are generally high; apparently there is little predation on the eggs which are well protected by layers of sand and stone (Manion and Hanson 1980). But, as the larvae emerge from the nest and move downstream to new habitat, they are susceptible to fish, insect, and crayfish predation. This is probably a period of high mortality. As ammocoetes increase in size, mortality rates decrease. In general, mortality of burrowed larvae is probably low, although they would be subject to predation during relocation in the stream.

Ecosystemic factors — Severe flooding may destroy nests, especially late June floods which could weaken the year-class by destroying most nests during a redistribution of stream bottom. Is there any data on such storms weakening a year-class? This factor would be less injurious on a stream with flood control devices. Flooding may also flush ammocoetes downstream, although there is some indication that larger ammocoetes are able to resist this action (Manion and Smith 1978). Flushed animals may be stranded in backwater areas or even on land. Such flushing action may also contribute to the larval populations found off those stream mouths where the lake habitat is favorable. On the other hand, periods of drought and low water may strand ammocoetes in areas of stagnating or evaporating water, or subject them to high temperatures which would increase mortality.

Water temperature (excessively high or low) during incubation could depress hatching success, but if sea lamprey nests are located in areas of groundwater flow with satisfactory temperatures, incubation temperatures would be stabilized.

S. H. Smith (USFWS, Ann Arbor, Michigan, retired, personal communication) believes that prior to deforestation and drainage of swamps in vast areas of the Great Lakes basin, streams were well-shaded, cool and clear, with steady discharges, and generally with water temperatures too cold for sea lamprey production. If restoration of similar conditions can be encouraged in appropriate areas, sea lamprey reproduction may be reduced. He also recommends accelerating the process through reforestation programs and protection of stream cover now present and suggests a study to verify the relationship before making any major effort to foster ecologic control by manipulating stream temperatures by reducing solar radiation. Information on the effects of reducing solar radiation on stream temperature is available.

Man-Made Controls

BIOLOGICAL CONTROL

Parasites, predators, and pathogens — It is generally conceded that the best subjects for biological control are organisms introduced into a new region without the large complex of parasites, predators, and pathogens that attack them in their native homes. These organisms often find large and virtually unexploited sources of food and therefore are able to expand their numbers enormously. Compared with the complex interrelations existing between an animal and its environment when the two have evolved together for generations, these immigrant animals present a relatively simple problem; their relations with their environment are incompletely established and are amenable to manipulation. Often the introduction of one new biotic agent will limit their numbers to a satisfactory level. Such newly introduced agents themselves assume a position in the new environment similar to that occupied by their host, and factors identical with those that ensured the success of the host will operate for them also; they are introduced into a new region without biotic agents to attack them; they find an abundance of food in the form of an epizootic host population; there are few other organisms utilizing the same food source to compete with them; they are free to expand their numbers to the limit of their food supply, i.e. their host. They eventually overexpand and deplete their food supply and thus bring about the control of the pest.

Elton (1958) discussed the explosive development of populations which follow their introduction into new areas without natural enemies and used the invasion of the Great Lakes by the sea lamprey as an example. The sea lamprey, an immigrant pest, appears to be a good prospect for control by the introduction of a biotic agent from its native habitat. Some information is available on the predators, parasites, and pathogens of sea lampreys in the Great Lakes (Applegate 1950; McLain 1951; Wilson and Ronald 1967), but to our knowledge, little research has been done on sea lampreys in their native habitat along the east coast of North America. Comparing population densities between their native habitat and their new habitat in the Great Lakes may indicate whether there is some degree of biological control being maintained in the native habitat.

As in all biological control work, priority should be placed on studying that portion of the native home of the pest species which most nearly resembles the region in the invaded area where control is desired. In addition to studies on parasites, predators, and diseases found attacking the sea lamprey (or its close relatives), the degree of host specificity of these organisms must be determined.

Whether biological control will be successful depends entirely on the species involved; their parasitic, predatory, and pathogenic complexes; the areas invaded; and the efforts put into a biological control campaign. Until an investigation is made, and something is known of the ecology and natural enemies of the pest in its original habitat, no opinion as to the possibilities of biological control is valid (Simmonds 1956).

The use of parasites, predators, and pathogens for control of pest species involves not only the importing of these enemies from their native home, but also the enhancement, by various means, of the effectiveness of natural enemies already present in the environment. Undoubtedly, the larval populations in the Great Lakes are regulated somewhat by natural forces, but to what degree parasites, predators, and diseases are involved is unknown.

Competitive displacement — If two species share a single common environmental requisite and one species for any reason exploits that requisite more efficiently than the other, this species should gradually take over a larger and larger proportion of that requisite and thus progressively deny it to the other, and displacement would follow (Turnbull 1967). The most logical competitor for the sea lamprey would be a nonparasitic lamprey. Native, nonparasitic lampreys would be of limited value as competitors as long as the toxicants TFM and Bayer 73 are used, since their numbers also are effectively reduced by chemical treatments (Schuldt and Goold 1980). Discovery of a compound that kills only sea lamprey larvae could make native lampreys effective competitors. If such a compound cannot be found, it may be possible to find and introduce nonparasitic species of lampreys that are not as susceptible to lampricides as the sea lamprey, and that may be able to increase in numbers and out-compete larval sea lampreys and eventually displace them or at least reduce their abundance. In analyzing the population dynamics of sea lamprey larvae, quality or abundance of food may be a limiting factor, but we must not ignore the possible role of social intolerance as a limiting factor.

GENETIC CONTROL

Sterile male technique — The sterile male method of controlling certain pests has been highly successful (Kilgore and Doutt 1967). Hanson and Manion (1980) describe the theory, the requirements for its successful application, and various ways the technique could be applied to the sea lamprey. The extent to which the sterility technique will be used in the sea lamprey control program will be contingent on the degree of progress that is made in the following areas:

1) It will be necessary to find satisfactory chemical sterilants, to develop safe methods of using them (Borkovec 1972), or find other ways of achieving sterility (ionizing radiation, immunological sterilization, etc.). Although bisazir, the lamprey chemosterilant (Hanson and Manion 1978), is mutagenic, it is highly reactive and is probably metabolized or excreted by the lamprey very rapidly (A. B. Borkovec, USDA, Beltsville, Maryland, and J. Allen, USFWS, La Crosse, Wisconsin, personal communication).
2) Application of the sterilization technique will require a thorough study of the biology, behavior, and population dynamics of the lamprey. Information on population densities, particularly during the spawning phase of their life cycle, is essential for fully evaluating the potential of the method. Marked, sterile animals may be useful in determining population densities through various mark–recapture studies. Examination of developing embryos in lamprey nests before and after release of sterile males will indicate the success of the technique.
3) A practical method of capturing and sterilizing a significant portion of the male population is essential. It may be possible to capture a large portion of spawning run lampreys through the use of portable assessment traps fished on only a few of the larger streams (J. W. Heinrich, USFWS, Marquette, Michigan, personal communication). The discovery of an attractant such as a sex pheromone would effectively increase the efficiency of the trapping effort (Teeter 1980).
4) A useful characteristic of the sterile male technique is that it becomes more effective as the natural population declines. Therefore, other control methods must be utilized to reduce the population to levels that could be manageable with the sterile male technique.

Other genetic approaches — In addition to external agents, such as chemosterilants or ionizing radiation, a variety of genetic mechanisms may be used to reduce sea lamprey populations or render them harmless. Within some insect species, crosses between various populations are sterile. Sterility is due to a cytoplasmic factor transmitted through the egg, which kills the sperm of the incompatible male after its entry into the egg. Control can be achieved by capture and release of the species into an area populated by incompatible crossing-types.

In some species there are a number of crossing-types or races which produce fertile females but only sterile males among their progeny. These sterile hybrids are excellent material for use in pest control because although the males are sterile, they are likely to be fully competitive and may show increased competitive mating ability because of hybrid vigor.

Other approaches which may be of some value are (1) upset the timing (delay or prevent) of metamorphosis, (2) remove the parasitic phase of sea lampreys through selective breeding, and (3) develop a monosex culture (all males) for use in a sterile-male release program.

OTHER CONTROL METHODS

Attractants and repellents — Teeter (1980) discussed the importance of pheromone communications in sea lampreys and their potential roles in sea lamprey control. An attractant would be of considerable value for guiding lampreys into target streams, and capturing and sterilizing spawning males. A repellent would not only increase the effectiveness of an attractant, but could be used to keep adult lampreys from spawning in streams that are difficult to treat with a lampricide.

Barrier dams and traps — Any method capable of reducing the spawning or larval habitat or the spawning population will be useful in an integrated control program. Hunn and Youngs (1980) discussed the history of physical barriers in the sea lamprey control program and examined their shortcomings. Attempts have been made to define structural and velocity criteria that can be used to design effective barrier dams. Davis and Shera (1971) observed migrating lampreys at Dennys Dam on the Saugeen River and found sea lampreys could not move upstream past the dam when the water velocity exceeded 375 cm/s at 24.2°C. Hanson (1978) determined that the burst swimming speed of sea lampreys exceeded 396 cm/s. Thus, the use of a velocity barrier may be impractical. Experiments by Youngs showed that a height of 30 cm stopped sea lamprey passage over dams (Hunn and Youngs 1980). Construction of barrier dams on carefully selected rivers is a part of the Great Lakes Fishery Commission's program to control sea lampreys.

Controlled light or sound waves could be investigated as possible alternatives to dams or as leading mechanisms to improve the efficiency of trapping devices. Barrier dams should be designed so that trapping devices can be used to assess spawning runs of sea lampreys.

Chemical toxicants — The present control program relies almost entirely on the use of selective toxicants. Their continued use is essential for controlling sea lamprey populations for some years to come. During this period we hope other effective control methods can be found which will reduce our reliance on selective toxicants.

INTEGRATED CONTROL

The advantages of integrating different methods of control should be considered in any control program. Sawyer (1980) concluded that the prospects for the integrated pest management of the sea lamprey were good, although there are many challenges ahead in the areas of research and implementation. Each method of control has its unique characteristics and will affect pest populations in certain ways. We must utilize all suitable techniques in an organized fashion so that one will compliment the other. We must not "put all our eggs in one basket" and rely on chemical control alone.

Differences Between Lampreys and Teleosts

The biological differences between the lamprey and teleost fish may be important for the development of new control methods. The lamprey lacks many of the specializations of higher vertebrates and also has some unique characteristics, and these may make it vulnerable to particular treatments. The following is an attempt to summarize the known physiological, biochemical, and behavioral differences. It is not comprehensive and should be revised as new information becomes available. For most of the organ systems the general similarities of lampreys and teleosts are stated, then the differences are listed, and finally suggestions are made for further research which may reveal additional differences, particularly those with potential for control methods.

SKELETAL SYSTEM

Lampreys lack a calcified skeleton (Hardisty and Potter 1971). The main support of the body is a primitive cartilaginous notochord, which decreases in length prior to spawning. Rib-like supports are absent, except in the fins and in the branchial basket. Much of the head skeleton of ammocoetes consists of mucocartilage (Johnels 1948). The teeth of adult lampreys are kerantinized, not calcified. The calcium reservoir of lampreys is probably lower than that of teleosts.

SKIN

The basic structure and properties of skin in lampreys (Lethbridge and Potter 1980) are similar to those of scaleless teleosts. Scales provide additional protection and coloration in some teleosts. Future research might test toxicants for their permeability through, and metabolism by, lamprey skin.

MUSCLE

Striated muscles of the lamprey are similar in ultrastructure, histochemistry, physiology, and pharmacology to those of teleosts (Rovainen 1979). The organization of myotomal muscle in subunits of slow and twitch fibers is peculiar to lampreys (Peters and MacKay 1961). As a consequence, the two types of muscle fibers are distributed rather uniformly through a cross section of the lamprey body. In teleosts, the slow red fibers are situated laterally and are used during slow swimming, while the fast twitch fibers constitute the rest of the myotome and are used during fast swimming and escape maneuvers. The lamprey has simple oblique myosepta for the attachment of myotomal muscle fibers, whereas the teleost has complex scalloping of segments and oblique lines of white fibers for optimal distribution of forces during swimming (Alexander 1969). The subunit organization in the lamprey prevents the direct access of the twitch fibers to oxygen and metabolites from the blood. Some twitch fibers lack direct motor innervation but are coupled to other fibers in the subunit (Teräväinen 1971). Two types of nerve endings occur on medial twitch fibers of lampreys but not of teleosts (Sakharov and Kashapova 1979). Peculiar slow muscle fibers are present in the velum of ammocoetes, as in the velum of the hagfish (Korneliussen and Nicolaysen 1973). Lamprey myotomal muscle is a major source of metabolites during the prespawning period. Whereas lipid is mobilized from other tissues in salmon, it is mobilized from muscle in lampreys (Hardisty and Potter 1971). Parvalbumins occur at high concentrations in teleost muscles and may help regulate intracellular Ca but are absent in lamprey muscle (Kohler et al. 1978). Topics for further research include muscle metabolism, fatigue of lamprey muscle during continued activity, and the control of muscle degeneration and growth during metamorphosis.

OSMOREGULATION

The regulation of osmolarity and the ionic composition of body fluids in fresh- and sea-water are similar in lampreys and teleosts (Morris 1972, 1980; F. W. H. Beamish 1980). The volume of interstitial fluid and the output of urine in freshwater are higher in lampreys than in teleosts. Lampreys take up K actively, and ammocoetes survive in very soft waters by means of strong uptake mechanisms for Na. The lack of a renal–portal circulation in the lamprey (Youson and McMillan 1971) may be a handicap for tubular secretion of urine in seawater. Topics for further research include differences in osmoregulation by anadromous and landlocked strains of sea lampreys, especially at critical life stages, and the contribution of food intake to water and salt balance in adults.

RESPIRATION

Although the mechanics of breathing in ammocoetes and adult lampreys are grossly different from those in teleosts, the fundamental features of respiration are similar in both groups of animals (Lewis 1980).

Ventilation of ammocoetes is produced by a primitive velum with enhancement of stroke volume by the branchial muscles (Rovainen and Schieber 1975). Ammocoetes have a lower resting oxygen consumption than do most teleosts of similar weight (Hill and Potter 1970). The survival of ammocoetes under conditions of low oxygen is related to the high oxygen affinity of their hemoglobins (Potter et al. 1970).

The tidal ventilation of water by adult lampreys is unique among fishes. The branchial muscles contract synchronously to exhale water, and the elastic recoil of the branchial basket produces passive inhalation. The neural control of respiration in the adult lamprey (Rovainen 1977) is simpler than that of teleosts and mammals.

Topics for further research include measurements of maximum aerobic capacities of adult lampreys and ammocoetes, possible ramjet ventilation in swimming adults, seasonal variations in respiration, the fraction of respiration through the skin in ammocoetes, diffusion capacity of the gills during TFM treatment, location of O_2 receptors, and identification of pattern generators for respiratory discharges.

CIRCULATION

The general pathway of blood circulation is similar in lampreys and teleosts (Fänge 1972). The blood volumes of ammocoetes and adult lampreys are larger than in teleosts (Morris 1980). Extensive venous sinuses accommodate much of the blood volume of adult lampreys (Tretjakoff 1927a). Specific sites of blood cell production are different in ammocoetes, adult lampreys (Percy and Potter 1977), and teleosts. Modulation of oxygen transport by organic phosphates in red blood cells has not been observed in lampreys. The monomeric hemoglobins of lampreys differ from the tetrameric hemoglobins of other vertebrates (Riggs 1972). Lamprey blood has a high iron content and multiple transferrins (Webster and Pollara 1969).

The heart of the adult lamprey is large compared to that of most other fish of the same size (Claridge and Potter 1974). It is surrounded by a capsule of cartilage and generates negative venous pressure (Johansen et al. 1973). Elastin is present in the ventral aorta of teleosts but not of lampreys (Sage and Gray 1979). The heart of the lamprey also differs from that of teleosts because its frequency of beating increases after stimulation of the vagus nerve and after application of nicotinic drugs (Augustinsson et al. 1956). Lampreys lack an organized sympathetic nervous system, but dense chromaffin cells occur in the heart and venous system (Rovainen 1979).

Topics for further research include the roles of multiple hemoglobins, the buffering capacity of the blood, the further identification of plasma proteins, and circulatory responses to chronic and acute changes in the environment.

FEEDING AND DIGESTION

The mechanisms of feeding are different in ammocoetes, adult lampreys, and teleosts. Ammocoetes collect particles of food from respiratory water on strands of mucus. Secretion from a primitive endostyle apparently contributes to the feeding mechanism. Although ammocoetes can select particles on the basis of size, shape, and adherent properties (Moore 1980), they probably cannot avoid the ingestion of inert and toxic particles. Unlike other suspension feeders, ammocoetes do not reduce their feeding rate in very high concentrations of particles (Mallatt 1980). This may occur because ventilation and feeding are closely coupled in the ammocoete, and excess particles may be absorbed in order to maintain respiration.

The adult lamprey is the only fish which feeds with a sucker and piston. The presence of buccal glands in the lamprey is also unusual. Some species of adult lampreys have the surprising ability to remove chunks of flesh from their victims (R. J. Beamish 1980). Blood and liquefied tissue are the typical food of sea lampreys, and large quantities can be ingested (Farmer 1980). The intestine of lampreys lacks mesenteric connections for nerve and blood supplies along most of its length. The capillary circulation of the gut in ammocoetes and in adult lampreys is poorly developed compared to that in teleosts (Percy and Potter 1979), and gross circulation to the gut in adult lampreys is provided by unusual vascular couples (Baxter and Robinson 1942). A system for biliary secretion is absent in adult lampreys (Youson and Sidon 1978). The bile compound of ammocoetes is different from those in higher vertebrates (Haslewood 1969).

Topics for further research include neurophysiology of attachment and feeding; functional roles of the teeth in adult lampreys of different species; taste receptors independent of olfaction, appetite, and satiation; and characterization of secretions from the endostyle and buccal glands and of digestive enzymes in ammocoetes and adult lampreys.

METABOLISM

The general metabolic pathways in lampreys and teleosts appear to be similar. Fat is a major reservoir for metabolites during nonfeeding periods in lampreys as in other animals. Specific storage areas for fat (Youson et al. 1979), such as the fat column in ammocoetes, can be different in lampreys and teleosts. Peculiar fat–glycogen cells occur in the meningeal tissues of ammocoetes and adult lampreys (Rovainen et al. 1971) and in other regions of the body (Tretjakoff 1927b). The cells around the brain produce glucose from glycogen during metabolic stress. Gluconeogenesis from glycerol to glycogen occurs in the body muscles of prespawning adult lampreys (Savina and Plisetskaya 1976). The intact liver is not required for glucose regulation in prespawning adults (Larsen 1978). The liver of ammocoetes lacks glucuronyl transferase activity, which inactivates TFM in teleosts (J. H. Howell, USFWS, Millersburg, Michigan, personal communication).

Future research should test the possibility that population densities of ammocoetes are limited by metabolites released into the silt. Such compounds could be collected from ammocoete colonies and identified and then applied to ammocoete beds to elicit migration. Other topics for research are energy metabolism, functions of the liver at different life stages, and metabolic differences of males and females. The detoxification mechanisms of ammocoetes and of adult lampreys should be surveyed in detail and compared to those of teleosts.

EMBRYOLOGY–DEVELOPMENT–GENETICS

Lampreys have a typical vertebrate embryological development, but it is more closely related to that of amphibians than of teleosts (Piavis 1971). Oöcytes are produced during the ammocoete stage, not in the adult stage as in most teleosts (Hardisty 1971). Some species of lampreys have the highest chromosome numbers of all vertebrates (Potter and Robinson 1971).

One important subject for further research is sex determination in lampreys. Sex ratios in lamprey populations vary, and knowledge of the controlling factors might allow manipulation to unfavorable extremes. Genetic research on lampreys is difficult because of high mortality and the long life cycle.

METAMORPHOSIS

The transformation of ammocoetes to adult lampreys (Youson 1980) is perhaps their most important difference from teleosts. Metamorphosis in amphibians is somewhat similar but differs with regard to hormonal control, early occurrence, and parts of the body affected. For instance, amphibian metamorphosis depends upon rising levels of thyroxine, but lamprey metamorphosis does not (Wright and Youson 1977).

Metamorphosis is one of the most important areas for further research on lampreys. All aspects should be investigated extensively. The induction and hormonal control of lamprey metamorphosis are especially relevant for providing new control methods. In particular, the roles of environmental temperature, the pituitary, and the pineal in lamprey metamorphosis should be studied in more detail.

ENDOCRINES

Many of the known vertebrate hormones have been detected in lampreys, namely, thyroxine, triiodothyronine, adrenaline, noradrenaline, dopamine, serotonin, melatonin, testosterone, estradiol, progesterone, several of the glucocorticosteroids, insulin, vasotocin, melanocyte-stimulating hormone, somatostatin, thyrotropin-releasing hormone, gonadotropin-releasing hormone, and activities resembling gonadotropin, corticotropin, glucagon, and gut hormones (L. Olesen Larsen, University of Copenhagen, Copenhagen, Denmark, and A. Gorbman, University of Washington, Seattle, Washington, personal communication). The following have not been detected: prolactin, oxytocin, renin, growth hormone, thyrotropin, and parathyroid hormone. The interrenal cells of lampreys are not encapsulated but are distributed along the body cavity and invade the kidney (Youson 1972). These presumed adrenocortical tissues have low rates of synthesis of steroid hormones from cholesterol (Weisbart et al. 1978). The levels of estradiol and testosterone in the blood of adult lampreys are ~1000-fold lower than in most higher vertebrates. The adenohypophysis in the lamprey has a peculiar embryonic origin from ectoderm behind the olfactory placode. In adult lampreys the adenohypophysis lacks both a portal circulation and direct innervation from the brain (Gorbman 1980). A urophysis is absent in lampreys, but small cells with secretory structure and with fluorescence for serotonin occur along the ventral spinal cord (Ochi et al. 1979). Corpuscles of Stannius are absent in the lamprey kidney (Nishimura et al. 1970).

Nearly all aspects of lamprey endocrinology deserve further research. Specific topics include regulation of growth, gut hormones, and mineral regulation.

IMMUNOLOGY

Lampreys resemble teleosts in their strong immune responses, chiefly cellular, to infection. Their wounds also heal effectively. The structure of immunoglobulins in lampreys differs from that in other animals (Good et al. 1972). The lamprey immune system responds to particulate antigens, and clearance of soluble antigens is poor (J. H. Howell, USFWS, Millersburg, Michigan, personal communication).

BEHAVIOR

The behavior of lampreys is more limited than that of teleosts. In the laboratory ammocoetes lie sedentary in burrows, and adults usually rest by hanging from their suckers, unless they are aroused by novel stimuli. In contrast to teleosts, lampreys have little or no capacity for learned behavior (W. O. Wickelgren, University of Colorado Medical Center, Denver, Colorado, unpublished data). Sea lampreys do not jump over barriers during migration and do not swim as rapidly as do many teleosts (Wardle 1975; Hunn and Youngs 1980). The endurance of adult lampreys during swimming for long periods is particularly poor (Beamish 1974). Lampreys lack both an air bladder for buoyancy control and paired fins for maneuvering. Many of the details of spawning behavior are different in lampreys (Manion and Hanson 1980) and in various teleosts.

Further research on the behavior of adult lampreys should identify the sensory cues for selection of prey and for activities associated with spawning. A topic for research on ammocoetes is the testing of conditions which promote movement from one site to another.

NERVOUS SYSTEM

The brain and spinal cord of the lamprey are relatively simple models for those of higher vertebrates (Rovainen 1979). The central nervous system has the same properties in lampreys and in teleosts with respect to physiology, organization, pharmacology, and metabolism. The most obvious difference of the lamprey nervous system is its minimal complexity. The cerebrum and cerebellum are particularly small, and the spinal cord has relatively few nerve cells and axons. Some other peculiarities of the lamprey nervous system compared to teleosts are the asymmetric enlargement of the right habenular nucleus, the lack of blood vessels inside the spinal cord, and the lack of iodine transport by the choroid plexus. A major deficiency in the lamprey nervous system is its lack of myelin. Conduction velocities of axons in the lamprey are slower than in teleosts, and the large unmyelinated axons take up space which might otherwise be used for additional nerve cells and synapses. Combined electrotonic–chemical synapses have been observed more frequently in lampreys than in teleosts. With regard to specific chemical transmitters, the synthesizing and hydrolyzing enzymes for acetylcholine are less active in the brain of the lamprey than in teleosts (Wächtler 1978), and aminergic projections from the brain to the spinal cord are weak or absent (Honma 1970). The Mauthner neuron can be recognized in both lampreys and teleosts, but it does not produce a tail flip response in lampreys, and it differs in several of its specific synaptic connections in the two types of animals (Rovainen 1979).

Research on the lamprey nervous system does not need much encouragement because its experimental and conceptual advantages are well known. Some research topics related to control include the mechanisms of arousal, changes in the nervous system during metamorphosis, and neuropharmacology directed toward behavioral control.

SENSORY SYSTEMS

In general the sensory systems of lampreys and teleosts are similar (Kleerekoper 1972). The eye of the adult lamprey has a typical vertebrate structure but differs in several details. A single photopigment is present at any stage, and color vision is probably absent. Vitamin A occurs as an ester in lamprey blood (Yoshihiro and Muto 1977). Photoreceptors in the lamprey have characteristics intermediate between rods and cones (Öhman 1976). Scotopic fusion frequency is lower in the lamprey than in any other vertebrate (Dreyfert et al. 1979). The interplexiform cells of the teleost retina are absent in the lamprey (Ehinger et al. 1977). Ganglion cells in the lamprey retina do not separate from the amacrine layer. The lamprey pupil does not dilate or constrict. Accommodation may be absent in the lamprey (Sivak and Woo 1975), but if present may be produced by muscles extrinsic to the eye (Franz 1932). Lampreys do not have rapid phases of nystagmus (Rovainen 1976).

The vestibular system of the lamprey lacks a horizontal semicircular canal, but the same function is served by the vertical cristae. The labyrinth of the lamprey contains peculiar ciliated chambers with constant fluid movement of unknown function. Hearing has not been tested in lampreys but may be defective as a result of the lack of an air–fluid interface, which is used effectively for sound detection by teleosts.

Some peculiarities of the olfactory system of the lamprey include the single nostril, the special mechanism for perfusing the olfactory sac, and the presence of olfactory sac tubules (Kleerekoper 1972).

The intramedullary neurons of the trigeminal mesencephalic root, which provide sensory innervation to teeth and jaw muscles in higher vertebrates, are absent in lampreys. Likewise, the lamprey lacks the prominent extramedullary cells of some teleosts (Bennett et al. 1959). Instead, the lamprey retains embryonic Rohon–Beard cells as the mechanosensory dorsal cells (Martin and Wickelgren 1971).

The importance of specific olfactory attractants and repellents for lamprey control has been recognized (Teeter 1980). Additional topics for further research include patterned vision in adult lampreys, responses to water currents and sound, proprioception, and chemosensitivity in ammocoetes.

Implications for Control

During its extensive discussions, the Task Force identified some implications which should be recognized in the sea lamprey control program.

At any significant levels of lamprey abundance, control appears most favorable during the embryonic and larval life stages because the number of transformers is insensitive to numbers of spawners or effective fecundity when these variables are above relatively low values.

Control efforts directed toward the spawning adults will become effective when the number of ammocoetes becomes limited by the number of spawners.

Since control of numbers by natural regulation probably occurs during ammocoete life and present controls are applied to ammocoete populations, evolution of an insensitivity to control is most likely to occur in the ammocoete life history. Increasing use of lentic environments may be such a change.

Sea lamprey control will be most effective in the long run if we better understand the lamprey life history and foraging strategies.

Conclusions

Since there is still time to develop supplementary and alternative control techniques while continuing the use of selective toxicants, efforts should be expanded in those areas considered most likely to succeed, combined with an accelerated search in new directions. For instance, the use of barrier dams on selected streams has been a valuable addition to the control arsenal (Hunn and Youngs 1980). Current research is actively pursuing the development of attractants and repellents (Teeter 1980) and the use of sterile males (Hanson and Manion 1980). These techniques show the most promise for the near future and their development should be accelerated. Over the longer term, the inherent natural differences in lamprey and teleost physiology provide fertile grounds for future research to develop new control methods.

It is hoped that this review of sea lamprey life history and potential regulatory mechanisms will stimulate the investigation of other alternatives.

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ALEXANDER, R. McN. 1969. The orientation of muscle fibres in the myotomes of fishes. J. Mar. Biol. Assoc. U.K. 49: 263–290.

APPLEGATE, V. C. 1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. U.S. Fish. Wildl. Serv. Fish. Bull. 55: 237 p.

ARON, W. I., AND S. H. SMITH. 1971. Ship canals and aquatic ecosystems. Science 174(4004): 13–20.

AUGUSTINSSON, K.-B., R FANGE, A. JOHNELS, AND E. ÖSTLUND. 1956. Histological, physiological and biochemical studies on the heart of two cyclostomes, hagfish (*Myxine*) and lamprey (*Lampetra*). J. Physiol. (London) 131: 257–276.

BAXTER, E. W., AND G. G. ROBINSON. 1942. The vascular couples of the hind-gut in the sub-class Petromyzontia. Proc. Zool. Soc. London 112: 138–[illegible]46.

BEAMISH, F. W. H. 1974. Swimming performance of adult sea lamprey, *Petromyzon marinus*, in relation to weight and temperature. Trans. Am. Fish. Soc. 103: 355–358.

1980. Osmoregulation in juvenile and adult lampreys. Can. J. Fish. Aquat. Sci. 37: 1739–1750.

BEAMISH, R. J. 1980. Adult biology of the river lamprey (*Lampetra ayresi*) and the Pacific lamprey (*Lampetra tridentata*) from the Pacific coast of Canada. Can. J. Fish. Aquat. Sci. 37: 1906–1923.

BENNETT, M. V. L., S. M. CRAIN, AND H. GRUNDFEST. 1959. Electrophysiology of supramedullary neurons in *Spheroides maculatus*. I. Orthodromic and antidromic responses. J. Gen. Physiol. 43: 159–188.

BIGELOW, H. B., AND W. C. SCHROEDER. 1948. Cyclostomes. Sears Found. Mar. Res., Yale Univ., Mem. 1(Part 1): 29–58.

BORKOVEC, A. B. 1972. Safe handling of insect chemosterilants in research and field use. Agric. Res. Serv., U.S. Dep. Agric. ARS-NE-2: 13 p.

BRAEM, R. A., AND H. H. MOORE. 1977. Sea lamprey control in the United States, p. 161–166. *In* Annu. Rep. to Great Lakes Fishery Commission. Great Lakes Fishery Commission, Ann Arbor, MI.

BUDD, J. C., AND F. E. J. FRY. 1960. Further observations on the survival of yearling lake trout planted in South Bay, Lake Huron. Can. Fish Cult. 26: 7–13.

CHRISTIE, W. J. 1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Board Can. 31: 827–854.

CHRISTIE, W. J., AND D. P. KOLENOSKY. 1980. Parasitic phase of the sea lamprey (*Petromyzon marinus*) in Lake Ontario. Can. J. Fish. Aquat. Sci. 37: 2021–2038.

CLARIDGE, P. N., AND I. C. POTTER. 1974. Heart ratios at different stages in the life cycle of lampreys. Acta Zool. (Stockholm) 55: 61–69.

DAHL, F. H. 1968. A surface tow net for the collection of parasitic-phase sea lampreys. Prog. Fish-Cult. 30: 183–184.

DAVIES, E. A. J. 1979. Canals and inland waterways, p. 753–763. *In* W. E. Preece [ed.] The New Encyclopaedia Britannica, 15th ed. Encyclopaedia Britannica, Inc., Chicago.

DAVIS, W. A., AND W. P. SHERA. 1971. Maximum swimming speed of spawning run sea lamprey. Rep. of Annu. Meeting, June 1971. Great Lakes Fish. Comm., Ann Arbor, MI. Append. X. p. 127.

DREYFERT, T., K. HOLMBERG, AND G. STRUWE. 1979. Critical fusion frequency of the river lamprey (*Lampetra fluviatilis*). Vision Res. 19: 551–553.

EHINGER, B., K. HOLMBERG, AND P. ÖHMAN. 1977. Aminergic and indoleamine accumulating neurons in the retina of the river lamprey (*Lampetra fluviatilis*). Acta Zool. (Stockholm) 58: 117–123.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen & Co., Ltd., London. 181 p.

Fänge, R. 1972. The circulatory system, p. 241–259. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys, Vol. II. Academic Press, London.

Farmer, G. J. 1980. Biology and physiology of feeding in adult lampreys. Can. J. Fish. Aquat. Sci. 37: 1751–1761.

Farmer, G. J., and F. W. H. Beamish. 1973. Sea lamprey (*Petromyzon marinus*) predation on freshwater teleosts. J. Fish. Res. Board Can. 30: 601–605.

Farmer, G. J., F. W. H. Beamish, and P. F. Lett. 1977. The influence of water temperature on the growth rate of the landlocked sea lamprey (*Petromyzon marinus*) and the associated rate of host mortality. J. Fish. Res. Board Can. 34: 1373–1378.

Farmer, G. J., F. W. H. Beamish, and G. A. Robinson. 1975. Food consumption of the adult landlocked sea lamprey, *Petromyzon marinus* L. Comp. Biochem. Physiol. 50A: 753–757.

Franz, V. 1932. Auge und Akkommodation von *Petromyzon* (*Lampetra*) *fluviatilis* L. Zool. Jabrb. 52: 118–178.

Gage, S. H. 1928. The lampreys of New York State—life history and economics, p. 158–191. *In* A biological survey of the Oswego River system. Suppl. 17th Annu. Rep. N.Y. Conserv. Rep. 1927.

Good, R. A., J. Finstad, and G. W. Litman. 1972. Immunology, p. 405–432. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys, Vol. II. Academic Press, London.

Goode, G. B. 1884. The lampreys — Petromyzontidae, p. 677–681. *In* G. B. Goode & Assoc. [ed.] The fisheries and the fishery industries of the U.S. Part 1(3). Gov. Print. Off., Wash.

Gorbman, A. 1980. Evolution of the brain–pituitary relationship: evidence from the Agnatha. Can. J. Fish. Aquat. Sci. 37: 1680–1686.

Great Lakes Fishery Commission. 1956. Annual Rep. of the Great Lakes Fishery Commission. Great Lakes Fish. Comm., Ann Arbor, MI. p. 29.

Hanson, L. H. 1978. Burst swimming speed of spawning-run sea lamprey (*Petromyzon marinus*). Res. Compl. Rep. Great Lakes Fish. Lab. Ann Arbor, MI. 11 p.

Hanson, L. H., and P. J. Manion. 1978. Chemosterilization of the sea lamprey (*Petromyzon marinus*). Great Lakes Fish. Comm. Tech. Rep. 29. 15 p.

1980. Sterility method of pest control and its potential role in an integrated sea lamprey (*Petromyzon marinus*) control program. Can. J. Fish. Aquat. Sci. 37: 2108–2117.

Hardisty, M. W. 1971. Gonadogenesis, sex differentiation and gametogenesis, p. 295–359. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys, Vol. 1. Academic Press, London.

Hardisty, M. W., and I. C. Potter. 1971. The general biology of adult lampreys, p. 127–206. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys, Vol. 1. Academic Press, London.

Haslewood, G. A. D. 1969. Comparative studies of bile salts: bile salts of the lamprey *Petromyzon marinus* L. Biochem. J. 114: 179–184.

Heinrich, J. W., J. G. Weise, and B. R. Smith. 1980. Changes in biological characteristics of the sea lamprey (*Petromyzon marinus*) as related to lamprey abundance, prey abundance, and sea lamprey control. Can. J. Fish. Aquat. Sci. 37: 1861–1871.

Hill, B. J., and I. C. Potter. 1970. Oxygen consumption in ammocoetes of the lamprey *Ichthyomyzon hubbsi* Raney. J. Exp. Biol. 53: 47–57.

Honma, S. 1970. Presence of monoaminergic neurons in the spinal cord and intestine of the lamprey, *Lampetra japonica*. Arch. Histol. Jpn. (Niigata Jpn.) 32: 383–393.

Hubbs, C. L., and K. F. Lagler. 1947. Fishes of the Great Lakes region. Cranbrook Inst. Sci., Bloomfield Hills, MI. 186 p.

Hunn, J. B., and W. D. Youngs. 1980. Role of physical barriers in the control of sea lamprey (*Petromyzon marinus*). Can. J. Fish. Aquat. Sci. 37: 2118–2122.

Johansen, K., C. Lenfant, and D. Hanson. 1973. Gas exchange in the lamprey, *Entosphenus tridentatus*. Comp. Biochem. Physiol., 44A: 107–119.

Johnels, A. G. 1948. On the development and morphology of the skeleton of the head of *Petromyzon*. Acta Zool. (Stockholm) 29: 139–279.

Johnson, B. G. H., and W. C. Anderson. 1980. Predatory-phase sea lampreys (*Petromyzon marinus*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37: 2007–2020.

Kilgore, W. W., and R. L. Doutt [ed.]. 1967. Pest control. Biological, physical, and selected chemical methods. Academic Press, New York and London. 477 p.

Kitchell, J. F., and J. E. Breck. 1980. Bioenergetics model and foraging hypothesis for sea lamprey (*Petromyzon marinus*). Can. J. Fish. Aquat. Sci. 37: 2159–2168.

Kleerekoper, H. 1972. The sense organs, p. 373–404. *In* M. W. Hardisty and I. C. Potter [ed.] The Biology of lampreys, Vol. II. Academic Press, London.

Kohler, L., J. A. Cox, and E. A. Stein. 1978. Sarcoplasmic calcium-bind proteins in prochordate and cyclostome muscle: characterization of a new protein from amphioxus. Mol. Cell. Biochem. 20: 85–94.

Korneliussen, H., and K. Nicolaysen. 1973. Ultrastructure of four types of striated muscle fibers in the Atlantic hagfish (*Myxine glutinosa* L.). Z. Zellforsch. 143: 273–290.

Lark, J. G. I. 1973. An early record of the sea lamprey (*Petromyzon marinus*) from Lake Ontario. J. Fish. Res. Board Can. 30: 131–133.

Larsen, L. O. 1978. Subtotal hepatectomy in intact or hypophysectomized river lampreys (*Lampetra fluviatilis* L.): effects on regeneration, blood glucose regulation, and vitellogenesis. Gen. Comp. Endocrinol. 35: 197–204.

Lawrie, A. H., and W. MacCallum. 1980. On evaluating measures to rehabilitate lake trout (*Salvelinus namaycush*) of Lake Superior. Can. J. Fish. Aquat. Sci. 37: 2057–2062.

Lethbridge, R. C., and I. C. Potter. 1980. Quantitative studies on the skin of the paired species of lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). J. Morphol. 164: 39–46.

Lett, P. F., F. W. H. Beamish, and G. J. Farmer. 1975. System simulation of the predatory activities of sea lampreys (*Petromyzon marinus*) on lake trout (*Salvelinus namaycush*). J. Fish. Res. Board Can. 32: 623–631.

Lewis, S. V. 1980. Respiration of lampreys. Can. J. Fish. Aquat. Sci. 37: 1711–1722.

Mallatt, J. 1980. A contribution to the feeding biology of the larval lamprey *Petromyzon marinus*. Ph.D. thesis, Univ. Chicago, IL.

Manion, P. J., and L. H. Hanson. 1980. Spawning behavior and fecundity of lampreys from the upper three Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1635–1640.

Manion, P. J., and A. L. McLain. 1971. Biology of larval sea lampreys (*Petromyzon marinus*) of the 1960 year class, isolated in the Big Garlic River, Michigan, 1960–65. Great Lakes Fish. Comm. Tech. Rep. 16: 35 p.

MANION, P. J., AND B. R. SMITH. 1978. Biology of larval and metamorphosing sea lampreys, *Petromyzon marinus*, of the 1960 year class in the Big Garlic River, Michigan, Part II, 1966–72. Great Lakes Fish. Comm. Tech. Rep. 30: 35 p.

MARTIN, A. R., AND W. O. WICKELGREN. 1971. Sensory cells in the spinal cord of the sea lamprey. J. Physiol. (London) 212: 65–83.

MCLAIN, A. L. 1951. Diseases and parasites of the sea lamprey, *Petromyzon marinus*, in the Lake Huron basin. Trans. Am. Fish. Soc. 81: 94–100.

MEYER, F. P., AND R. A. SCHNICK. 1980. Potential problems in the registration of sea lamprey (*Petromyzon marinus*) control agents. Can. J. Fish. Aquat. Sci. 37: 2093–2102.

MOORE, H. H., F. H. DAHL, AND A. K. LAMSA. 1974. Movement and recapture of parasitic-phase sea lampreys (*Petromyzon marinus*) tagged in the St. Marys River and Lakes Huron and Michigan, 1963–67. Great Lakes Fish. Comm. Tech. Rep. 27: 19 p.

MOORE, J. W., AND J. M. MALLATT. 1980. Feeding of larval lamprey. Can. J. Fish. Aquat. Sci. 37: 1658–1664.

MORMAN, R. H. 1979. Distribution and ecology of lampreys in the Lower Peninsula of Michigan, 1957–75. Great Lakes Fish. Comm. Tech. Rep. 33: 59 p.

MORRIS, R. 1972. Osmoregulation, p. 193–239. *In* M. W. Hardisty AND I. C. POTTER [ed.] The biology of lampreys, Vol. II. Academic Press, London.

1980. Blood composition and osmoregulation in ammocoete larvae. Can. J. Fish. Aquat. Sci. 37: 1665–1679.

NISHIMURA, H., M. OGURI, M. OGAWA, H. SOKABE, AND M. IMAI. 1970. Absence of renin in kidneys of elasmobranchs and cyclostomes. Am. J. Physiol. 218: 911–915.

OCHI, J., T. YAMAMOTO, AND Y. HOSOYA. 1979. Comparative study of the monamine neuron system in the spinal cord of the lamprey and hagfish. Arch. Histol. Jpn. (Niigata Jpn.) 42: 327–336.

ÖHMAN, P. 1976. Fine structure of photoreceptors and associated neurons in the retina of *Lampetra fluviatilis* (Cyclostomi). Vision Res. 16: 659–662.

PEARCE, W. A., R. A. BRAEM, S. M. DUSTIN, AND J. J. TIBBLES. 1980. Sea lamprey (*Petromyzon marinus*) in the Lower Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1802–1810.

PERCY, R., AND I. C. POTTER. 1977. Changes in haemopoietic sites during the metamorphosis of the lampreys *Lampetra fluviatilis* and *Lampetra planeri*. J. Zool. (London) 183: 111–123.

1979. The intestinal blood circulation in the river lamprey, *Lampetra fluviatilis*. J. Zool. (London) 187: 415–431.

PETERS, A., AND B. MACKAY. 1961. The structure and innervation of the myotomes of the lamprey. J. Anat. 95: 575–585.

PIAVIS, G. W. 1972. Embryology, p. 361–400. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys, Vol. II. Academic Press, London.

POTTER, I. C. 1980. Ecology of larval and metamorphosing lampreys. Can. J. Fish. Aquat. Sci. 37: 1641–1657.

POTTER, I. C., B. J. HILL, AND S. GENTLEMAN. 1970. Survival and behaviour of ammocoetes at low oxygen tensions. J. Exp. Biol. 53: 59–73.

POTTER, I. C., AND E. S. ROBINSON. 1972. The chromosomes, p. 279–293. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys, Vol. II. Academic Press, London.

PURVIS, H. A. 1979. Variations in growth, age at transformation, and sex ratio of sea lampreys reestablished in chemically treated tributaries of the Upper Great Lakes. Great Lakes Fish. Comm. Tech. Rep. 35: 36 p.

1980. Effects of temperature on metamorphosis and the age and length at metamorphosis in sea lamprey (*Petromyzon marinus*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1827–1834.

RIGGS, A. 1972. The haemoglobins, p. 261–286. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys, Vol. II. Academic Press, London.

ROVAINEN, C. M. 1976. Vestibulo-ocular reflexes in the adult sea lamprey. J. Comp. Physiol. 112: 159–164.

1977. Neural control of ventilation in the lamprey. Fed. Proc. 36: 2386–2389.

1979. Neurobiology of lampreys. Physiol. Rev. 59: 1007–1077.

ROVAINEN, C. M., G. E. LEMCOE, AND A. PETERSON. 1971. Structure and chemistry of glucose-producing cells in meningeal tissue of the lamprey. Brain Res. 30: 99–118.

ROVAINEN, C. M., AND M. H. SCHIEBER. 1975. Ventilation of larval lampreys. J. Comp. Physiol. 104: 185–203.

SAGE, H., AND W. R. GRAY. 1979. Studies on the evolution of elastin — 1. Phylogenetic distribution. Comp. Biochem. Physiol. B64: 313–327.

SAKHAROV, D. A., AND L. A. KASHAPOVA. 1979. The primitive pattern of the vertebrate body muscle innervation: ultrastructural evidence for two synaptic transmitters. Comp. Biochem. Physiol. A62: 771–776.

SAVINA, M. V., AND E. M. PLISETSKAYA. 1976. Synthesis of glycogen from glycerin in isolated tissues of the river lamprey *Lampetra fluviatilis*. J. Evol. Biochem. Physiol. (transl.) 12: 257–259.

SAWYER, A. J. 1980. Prospects for integrated pest management of the sea lamprey (*Petromyzon marinus*). Can. J. Fish. Aquat. Sci. 37: 2081–2092.

SCHULDT, R. J., AND R. GOOLD. 1980. Changes in the distribution of native lampreys in Lake Superior tributaries in response to sea lamprey (*Petromyzon marinus*) control, 1953–77. Can. J. Fish. Aquat. Sci. 37: 1872–1885.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Fish. Res. Board Can. 184: 966 p.

SIMMONDS, F. J. 1956. The present status of biological control. Can. Entomol. 88: 553–563.

SIVAK, J. G., AND G. C. S. WOO. 1975. Accommodative lens movement in holosteans (*Amia calva* and *Lepisosteus osseus oxyurus*) and in the sea lamprey (*Petromyzon marinus*). Can. J. Zool. 53: 516–520.

SPANGLER, G. W. 1974. Mortality factors and dynamics of a Lake Huron lake whitefish population. Ph.D. thesis, Dep. Zool., Univ. Toronto, Ont. 130 p.

SPANGLER, G. W., AND J. J. COLLINS. 1980. Response of lake whitefish, *Coregonus clupeaformis*, to the control of sea lamprey (*Petromyzon marinus*) in Lake Huron. Can. J. Fish. Aquat. Sci. 37: 2039–2046.

TEETER, J. 1980. Pheromone communication in sea lampreys (*Petromyzon marinus*): implications for population management. Can. J. Fish. Aquat. Sci. 37: 2123–2132.

TERÄVÄINEN, H. 1971. Anatomical and physiological studies on muscles of lamprey. J. Neurophysiol. 34: 954–973.

TRETJAKOFF, D. 1927a. Das Gefässsystem in Keimengebiet des Neunauges. Gegen. Morphol. Jahrb. 58: 209–264.

1927b. Die Fettglycogenzellen beim Neunauge. Anat. Anz. 63: 72–82.

TURNBULL, A. L. 1967. Population dynamics of exotic insects. Bull. Entomol. Soc. Am. 13(4): 333–337.

WÄCHTLER, K. 1978. The regional distribution of cholinacetyl transferase and acetylcholinesterase in the brain of the lamprey (*Petromyzon fluviatilis*). Comp. Biochem. Physiol. C61: 411–413.

WARDLE, C. S. 1975. Limit of fish swimming speed. Nature 255: 725–727.

WEBSTER, R. O., AND B. POLLARA. 1969. Isolation and partial characterization of transferrin in the sea lamprey, *Petromyzon marinus*. Comp. Biochem. Physiol. 30: 509–527.

WEISBART, M., J. H. YOUSON, AND J. P. WIEBE. 1978. Biochemical, histochemical, and ultrastructural analysis of presumed steroid-producing tissues in the sexually mature sea lamprey, *Petromyzon marinus* L. Gen. Comp. Endocrinol. 34: 26–37.

WELLS, L. 1980. Lake trout (*Salvelinus namaycush*) and sea lamprey (*Petromyzon marinus*) populations in Lake Michigan, 1971–78. Can. J. Fish. Aquat. Sci. 37: 2047–2051.

WILSON, K. A., AND K. RONALD. 1967. Parasite fauna of the sea lamprey (*Petromyzon marinus* von Linné) in the Great Lakes region. Can. J. Zool. 45: 1083–1092.

WRIGHT, G. M., AND J. H. YOUSON. 1977. Serum thyroxine concentrations in larval and metamorphosing anadromous sea lamprey, *Petromyzon marinus* L. J. Exp. Zool. 202: 27–32.

YOSHIHIRO, S., AND Y. MUTO. 1977. Vitamin A transport in plasma of the non-mammalian vertebrates: isolation and partial characterization of piscine retinol-binding protein. J. Lipid Res. 18: 679–691.

YOUNGS, W. D. 1980. Estimate of lamprey-induced mortality in a lake trout (*Salvelinas namaycush*) population. Can. J. Fish. Aquat. Sci. 37: 2151–2158.

YOUSON, J. H. 1972. Structure and distribution of interstitial cells (presumptive interrenal cells) in the opisthonephric kidneys of larval and adult sea lamprey, *Petromyzon marinus* L. Gen. Comp. Endocrinol. 19: 56–68.

1980. Morphology and physiology of lamprey metamorphosis. Can. J. Fish. Aquat. Sci. 37: 1687–1710.

YOUSON, J. H., AND D. B. MCMILLAN. 1971. Intertubular circulation in the opisthonephric kidneys of adult and larval sea lamprey, *Petromyzon marinus* L. Anat. Rec. 170: 401–411.

YOUSON, J. H., J. LEE, AND I. C. POTTER. 1979. The distribution of fat in larval, metamorphosing, and young adult anadromous sea lampreys, *Petromyzon marinus* L. Can. J. Zool. 57: 237–246.

YOUSON, J. H., AND E. W. SIDON. 1978. Lamprey biliary atresia: first model system for the human condition. Experientia 34: 1084–1086.

Interactions between Sea Lamprey (*Petromyzon marinus*) and their Forage Base. A Report from the SLIS Stock Effects Task Force[1,2]

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LAWRIE, A. H. (with appendices by W. D. Youngs, R. Morris, and G. R. Spangler). 1980. Interactions between sea lamprey (*Petromyzon marinus*) and their forage base. A report from the SLIS Stock Effects Task Force. Can. J. Fish. Aquat. Sci. 37: 2193–2196.

A task force of participants convened during the course of the Sea Lamprey International Symposium considered the implications, for management of Great Lakes fisheries, of information provided about known interactions between feeding sea lampreys and the stocks of fish on which they prey. A weighted series of recommendations identified the need for more information or for changes in management practice.

Key words: sea lamprey, Great Lakes, Finger Lakes, fishery management, stock concept

LAWRIE, A. H. (with appendices by W. D. Youngs, R. Morris, and G. R. Spangler). 1980. Interactions between sea lamprey (*Petromyzon marinus*) and their forage base. A report from the SLIS Stock Effects Task Force. Can. J. Fish. Aquat. Sci. 37: 2193–2196.

Lors du Colloque international sur la grande lamproie marine, un groupe de travail recruté parmi les participants s'est réuni pour considérer les implications, pour la gestion des pêches des Grands Lacs, de l'information fournie concernant les interactions entre l'alimentation de la grande lamproie marine et les stocks de poissons proies qu'elles attaquent. Des recommandations, par ordre de priorité, précisent le besoin de plus d'information ou de changements dans la gestion.

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FROM the sea lamprey control program and its many associated studies has come a wealth of observations regarding interactions between lamprey and their prey in the Great Lakes and related waters. The Stock Effects Task Force was asked to consider these and offer recommendations as to how the information might be used to render the program more effective.

Of the recommendations presented here, few were unanimously subscribed to by all members of the Task Force. Many have been compounded from several suggestions and, if that ensures that they are no longer recognizable verbatim, it also ensures that not much that stood the test of discussion has been entirely omitted. We *have* omitted considerations of how to explain and sell these and related ideas to legislators and the public, not because those activities are not vital, but because they begin, in our judgment, where this Symposium leaves off. Accordingly they have been left to the Great Lakes Fishery Commission and the managers in the cooperating governments.

We take as given the continuance of sea lamprey control, the planting of hatchery-reared salmonids, and constraints on human exploitation of fish stocks in a manner which is, at once, conservative yet seeks to provide the paying public as much as can be safely taken. Accordingly we did not spend much time on subjects which relate to fine tuning of these existing activities. Instead we tried to pull together our ideas regarding the nature and predictability of the relationships between them. In more homely terms we thought about how lamprey control, salmonid stocking, and control of exploitation conspire to determine what is in the lake — today and tomorrow.

In retrospect, what evolved from our discussions hinged on recognition of the paramount importance of the predator/prey ratio to the outcome of any scenario we examined. It led us directly to examine two areas of concern, namely, what did we need to know about sea lamprey and the factors controlling their production and activity on the one hand, and what did we need to know about prey and their responses to sea lamprey predation on the other. Because of the apparent differences in the system responses in the Upper Great Lakes and lakes Cayuga and Seneca, we concentrated our thinking on how these might be exploited

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[1] This paper forms part of the Proceedings of the Sea Lamprey International Symposium (SLIS) convened at Northern Michigan University, Marquette, Michigan, July 30–August 8, 1979.

[2] Chairman: A. H. Lawrie; Members: W. C. Anderson, H. Auvinen, R. A. Braem, G. Farmer, C. M. Fetterolf, P. A. Gilderhus, R. Goold, J. H. Howell, B. G. H. Johnson, K. Kainua, J. Mallatt, R. H. Morman, R. Morris, W. A. Pearce, R. J. Poff, P. C. Rugen, A. Sawyer, D. Talhelm, R. L. Torblaa, L. Wells, W. Westman, W. Youngs.

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to extend our understanding of the dynamics of the processes concerned. In particular, we looked for missing information (in the military sense of evaluated data) and for ideas to explain flagrant differences in the apparent behavior of the lamprey/prey systems in their several situations.

Sea Lamprey Production in Streams

Since lamprey production is an obvious determinant of the predator/prey ratio, we asked first whether there were obvious differences between the Upper Lakes lamprey production system and that of the Finger Lakes and similar, if less clear-cut, Lower Lake situations. As a group, we had an intuitive feeling that the Lower Lakes/Finger Lakes system simply produce far fewer lamprey per unit volume of lake so that differences may be, in part at least, matters of scale. Accordingly, we suggest that available data be assembled by the agents and such collaborators as they can dragoon to:

RECOMMENDATION 1: *Compare the number and size of sea lamprey producing streams tributary to each of the lakes containing sea lamprey and express these data on a per-unit-lake-volume basis.*

In the process, it would be highly desirable to extend the fine start towards definition of a sea lamprey spawning stream contained in the paper by Morman et al. (1980) at this Symposium by obtaining any needed data to define better the hydrology, hydrochemistry, thermal regimes, and productivity of these streams since these things may not only define their production of sea lamprey but also the time to transformation and hence the turnover rate. Accordingly:

RECOMMENDATION 2: *In assembling information on lamprey streams, round out, as necessary, a full description of their annual cycles of hydrology, hydrochemistry, thermal regime, and productivity.*

Biology of Feeding Phase Sea Lamprey

We were also impressed with the need to know more about the distribution, movement, and behavior of feeding phase sea lamprey in all these waters. The excellent work reported by Johnson and Anderson (1980) to this Symposium not only deserves commendation but continuance, and emulation in lakes off the Great Lakes system. We know of no other way to approach the question of the seasonal distribution of growing lamprey, their movements, food supplies, growth, and ultimately the questions of energetics, with its implications of scope for growth and fecundity, and of the cues to which the lamprey respond in making these movements. Obviously, the last could relate to questions of attractants and repellants in ways of significance to improving the control program.

RECOMMENDATION 3. *The assemblage of information on the distribution, size, sex, associated prey, and other information regarding Great Lakes sea lamprey stocks should be maintained and extended to off-system sea lamprey lakes as soon as possible.*

Management of Fish Stocks

As far as questions of managing the prey stocks in sea lamprey infested lakes were concerned, there was tacit admission of the fact that the sea lamprey was here to stay and that our problem is one of learning how to manage in the face of this stress. The problems, the solutions, and the costs of doing so in each of the Great Lakes and those off-system can be expected to be different. Further, the documented movements of both sea lamprey and prey between lakes suggest that it may well be necessary to treat the lakes as a system, concentrating efforts where and when they are needed so far as political realities permit. This is already being done by the lamprey control agents but not by those who rear and plant fish. As we believe this to be more properly the concern of another task force, we have not stated our concern as a recommendation, but it is obvious that the Great Lakes Fishery Commission has a predominant role to play here.

Each lake now contains at least the wreck of what can be assumed to have been a coadapted system conditioned by 10 000 yr of postglacial evolution. It is such a coadapted system that in the long run we want to rebuild and in doing so we cannot afford to use nonadapted species or maladapted stocks. We have already had sufficient experience with the former in the Great Lakes to have developed a decidedly cautious approach, but we are worried over the lack of attention paid to the latter in our present stocking programs. It is time, we believe, to do two things:

RECOMMENDATION 4. *Review present hatchery practices, especially when these involve the use of brood stocks, to confirm that they have not become inbred, highly selected, domestic stocks with, perhaps, a sharply reduced fitness for the role we expect them to play.*

RECOMMENDATION 5: *Explore the potential of other genetically identifiable salmonid stocks, including those from the off-system lakes where lake trout and sea lamprey seem to coexist successfully, for furthering rehabilitation efforts. Clearly, this will require systematic research to find, identify, evaluate, and test such stocks.*

A related concern stems from the observations of many people at this Symposium that we may inadvertently and easily generate other predator/prey systems like that suggested at this Symposium by Walters et al. (1980) for lamprey/prey systems, e.g. salmonid populations which the forage base cannot sustain. In particular, alewife, like clupeids elsewhere, may prove highly vulnerable in the end. Our experience to date suggests that their reduction might be compensated for by material and desirable increases in stocks of the lesser coregonids, especially lake herring and ciscoes. However, if the transition were to be catastrophic in its terminal stages, it would be highly desirable to be in a position to flood the system with viable, well-fitted coregonid stocks carrying genetic markers to allow evaluation of their contribution to the establishment of naturally reproducing stocks. Accordingly:

RECOMMENDATION 6: *Do the necessary research to find, identify, and evaluate coregonid stocks, especially of the subgenus* Leucichthys *which might serve to supplement and diversify the forage base available to salmonids in the Great Lakes and develop the necessary technology for their mass rearing to whatever size is needed to ensure reasonable survival on planting.*

Great Lakes–Finger Lakes Contrasts

Our perplexity over the conflicting (?) experience reported from the Upper Lakes and the Finger Lakes of New York State might be lessened by the systematic evaluation of a number of concerns identified by the Task Force. To do so would not only satisfy our intellectual curiosity but provide significant input to the consideration of Finger Lakes lake trout stocks for planting in the Upper Lakes. Accordingly:

RECOMMENDATION 7: *Direct and detailed comparisons of the forage base employed by the sea lamprey at each stage of its parasitic life in all our waters need to be assembled, supplemented if need be, and evaluated, not only as an aid in defining the energetics of growth and hence both the mortality per attack and the fecundity of the lamprey, but also as a basis for the more general concern to ensure the security of the forage base referred to in the last Recommendation. Other species may well be as important as the coregonids focused on there.*

RECOMMENDATION 8: *A careful comparison of the exploitation history of lake trout in the Finger Lakes and the Great Lakes needs to be carried out to determine whether the resulting size distributions could, of themselves, be sufficiently different to have reduced fecundity in the Great Lakes situation to a level much closer to the catastrophe fold than has ever been the case in the Finger Lakes.*

RECOMMENDATION 9: *Mechanisms which might account for differential probability of a lake trout surviving a sea lamprey attack need to be explored and we recommend pursuit of the two proposals appended, one by Bill Youngs and Ron Morris, the other by Geo. Spangler and Bill Youngs. Both have the merit of being directly testable as well as the potential of affording some insight into a complex problem.*

Priorities

Our sense of priorities has been derived from two considerations roughly stated as importance and feasibility. We hold it will be vitally important to begin to take better account of the "stock problem" in planting fish and therefore accord a very high priority to Recommendations 4 through 6 and perhaps 7 too. Because it is so difficult to obtain information about the parasitic phase, we urge again continuance and extension of Herb Johnson's and Bill Anderson's work as in Recommendation 3. Because we believe that what can be simply tested should be, and the sooner the better, we attach a high priority to the Youngs/Morris, Spangler/Youngs proposals referred to in Recommendation 9. As for the balance, they are important and the effort involved to implement them should be explored by the agents. It may be that most of the data are now in hand. If so, their assembly and evaluation as soon as possible is desirable. If not, they should take their place in the queue of work for the future whenever the needed resources can be found.

Appendix A

A Possible Role of Water Chemistry in Lamprey Prey Interactions

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The observed effect of lamprey on host or prey species is not consistent between the Upper Great Lakes and several New York lakes. A possible explanation for this observation may be linked to the chemical composition of lake water. For example, the chloride ion concentration is unusually high in Cayuga and Seneca lakes compared to levels found in Lake Superior. One might speculate that a lamprey would have to spend more energy to maintain its chloride ion in water with a lower chloride concentration. It is conceivable that host species are a more important source of ions in water of low ion concentration than in water of higher ion concentration.

Other ions may serve to condition survival of the host in an analogous fashion. For example, the role of calcium in osmoregulatory processes has been known for some time. The additional stress caused by lamprey attack in water of low ion concentration may be of sufficient magnitude to cause mortality. Other physiological processes may be influenced by the other ions and cause additional stress or increase feeding time in situations where such ions are limited.

There would seem to be a number of testable hypotheses under experimental conditions. Such experiments would contribute significantly to understanding the interaction between lamprey and its host.

Another significant factor may be the effect of wounds on permeability and the effect of ions on wound permeability. Again, using Na_{22}, this is a testable situation.

Appendix B

A Hypothesis Relating Lamprey-Induced Mortality and Prey Growth Rate

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In examining the set of SLIS lakes, we are impressed by the apparent coincidence between lamprey-mark frequencies and growth rates of prey fish. It appears that for some prey species, the probability of surviving an individual lamprey attack is conditioned by the growth rate of the host. Christie and Kolenosky (1980, Fig. 6) demonstrated that growth increments in lake whitefish were negatively correlated with the proportion of the stock wounded by lamprey. Spangler and Collins (1980) found that the most rapidly growing stocks of Lake Huron whitefish were also most greatly affected by lamprey predation. Youngs (1980) reported no significant lamprey-induced mortality in a slow-growing lake trout population in Cayuga Lake. This is in contrast to the situation in Lake Superior where trout growth is rapid and lamprey-induced mortality remains high. Lamprey-induced mortality in lake whitefish is coincident with the period of maximum growth rate in northern Lake Huron (Spangler 1974). We infer from these observations that rapidly growing host fish are more likely to succumb to the effects of a single lamprey attack than are slow-growing hosts. This suggests a mechanism by which intensive exploitation with its concomitant compensatory increase in growth rate may have "softened up" the Great Lakes fish community for catastrophic decline (Regier and Loftus 1972).

There are a number of mechanisms which might account for the lethal effect on rapidly growing fish. We speculate that prey fish committed by hormonal regulation to a rapid growth regime may be unable to shunt their energy allocations into tissue replacement in time to prevent death. Alternatively, the host may be elaborating gonadal tissue prior to the onset of the fall spawning season. It may be relevant that spring spawning species, both native and exotic, were not extirpated during the upper lakes fish stock declines.

This suggests another interesting class of testable hypotheses relating to lamprey selection of host fish. It is possible that lampreys seek hosts according to level of maturation or energy content rather than by growth rate alone. This might be reflected in differential wounding of mature and immature fish and should be detectable in historical data presently on hand.

CHRISTIE, W. J., AND D. P. KOLENOSKY. 1980. Parasitic phase of the sea lamprey (*Petromyzon marinus*) in Lake Ontario. Can. J. Fish. Aquat. Sci. 37: 2021–2038.

JOHNSON, B. G. H., AND W. C. ANDERSON. 1980. Predatory-phase sea lampreys (*Petromyzon marinus*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37: 2007–2020.

MORMAN, R. H., D. W. CUDDY, AND P. C. RUGEN. 1980. Factors influencing the distribution of sea lamprey (*Petromyzon marinus*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1811–1826.

REGIER, H. A., AND K. H. LOFTUS. 1972. Effects of fisheries exploitation on salmonid communities in oligotrophic lakes. J. Fish. Res. Board Can. 29: 959–968.

SPANGLER, G. 1974. Mortality factors and dynamics of a Lake Huron whitefish population. Ph.D. thesis, University of Toronto, Toronto, Ont. 130 p.

SPANGLER, G. R., AND J. J. COLLINS. 1980. Response of lake whitefish (*Coregonus clupeaformis*) to the control of sea lamprey (*Petromyzon marinus*) in Lake Huron. Can. J. Fish. Aquat. Sci. 37: 2039–2046.

WALTERS, C. J., G. STEER, AND G. SPANGLER. 1980. Responses of lake trout (*Salvelinus namaycush*) to harvesting, stocking, and lamprey reduction. Can. J. Fish. Aquat. Sci. 37: 2133–2145.

YOUNGS, W. D. 1980. Estimate of lamprey-induced mortality in a lake trout (*Salvelinus namaycush*) population. Can. J. Fish. Aquat. Sci. 37: 2151–2158.

Assessment of Lamprey and Fish Stocks in the Great Lakes in Relation to Control of the Sea Lamprey (*Petromyzon marinus*): Report from the SLIS Assessment Measurements Task Force[1,2]

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MAITLAND, P. S. 1980. Assessment of lamprey and fish stocks in the Great Lakes in relation to control of the sea lamprey (*Petromyzon marinus*): report from the SLIS Assessment Measurements Task Force. Can. J. Fish. Aquat. Sci. 37: 2197–2201.

Available and potential methodology for assessing lamprey and prey fish populations is related to existing and future requirements of the sea lamprey control program of the Great Lakes Fishery Commission (GLFC). For lamprey, we recommend that the classification of Great Lakes tributaries according to their potential for larval production and the quality of lamprey attack data should be improved and standardized; standardized collections of spawning run adults should be continued; research should be encouraged on attractants and repellents, a male sterilization program, and the biology of parasitic phase animals. For fish, we recommend that more emphasis be given to the precision and standardization of estimates to allow better comparison between places and years, and the assessment of fish stocks other than major prey species; the GLFC support an evaluation program of an important prey species; and that other assessment methods (e.g. acoustic; counts of entrained fish) be explored. Because lamprey control is a long-term process that may span periods of environmental change, monitoring of physical, chemical, and biotic factors should be encouraged. Research on the impact of lampricides on nontarget organisms should be expanded. We also discuss and offer suggestions on the future of sea lamprey control.

Key words: stock assessment, fishery surveys, methodology, populations control, proposed research

MAITLAND, P. S. 1980. Assessment of lamprey and fish stocks in the Great Lakes in relation to control of the sea lamprey (*Petromyzon marinus*): report from the SLIS Assessment Measurements Task Force. Can. J. Fish. Aquat. Sci. 37: 2197–2201.

La méthodologie actuelle et potentielle d'évaluation des populations de lamproies et de poissons proies est liée aux exigences présentes et futures du programme de contrôle de la grande lamproie marine de la Commission des pêcheries des Grands Lacs (CPGL). Pour ce qui est de la lamproie, nous recommandons que la classification des tributaires des Grands Lacs selon leur potentiel de production larvaire et que la qualité des données sur les attaques des lamproies soient améliorées et normalisées; que les collections normalisées de remontées reproductrices d'adultes soient continuées; que la recherche sur les substances attractives et répulsives, sur un programme de stérilisation des mâles et sur la biologie de la phase parasitaire des lamproies soit encouragée. Quant aux poissons, nous recommandons qu'on accorde plus d'attention à la précision et à la normalisation des estimations afin d'obtenir une meilleure comparaison entre localités et années, ainsi qu'à l'évaluation des stocks de poissons autres que les principales espèces proies; que la CPGL se charge d'un programme d'évaluation d'une importante espèce proie; et que d'autres méthodes d'évaluation (e.g. acoustiques; comptages de poissons entraînés dans les conduites) soient explorées. Étant donné que le contrôle de la grande lamproie marine est une opération à long terme qui peut chevaucher des périodes de changement du milieu, la surveillance continue des facteurs physiques, chimiques et biotiques devrait être encouragée. La recherche sur l'impact des lampricides sur les organismes non visés devrait être élargie. Nous examinons et offrons des suggestions concernant l'avenir du contrôle de la grande lamproie marine.

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[1] This paper forms part of the Proceedings of the Sea Lamprey International Symposium (SLIS) convened at Northern Michigan University, Marquette, Michigan, July 30–August 8, 1979.

[2] Chairman: P. S. Maitland; Members: R. Bishop, J. J. Collins, D. W. Cuddy, J. B. Hunn, E. Ikonen, J. Jokiel, E. L. King, G. R. King, J. H. Kutkhun, W. MacCallum, R. McDonald, P. J. Manion, H. H. Moore, J. D. Moore, G. W. Piavis, R. J. Schuldt, K. Sjöberg, G. R. Spangler, J. J. Tibbles, V. D. Vladykov, L. Wells, W. O. Wickelgren, A. T. Wright.

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THE Assessment Measurements Task Force was asked to address questions of sampling design, cost and precision with respect to the assessment of lamprey abundance, prey fish abundance, interactions between fish and lampreys, and the efficacy of control procedures. The Task Force was also asked to question how lamprey control might be further enhanced and to provide guidelines for an assessment strategy that will result in improved estimates of the status of the fish community.

There have been several meetings of the full Task Force and of its subgroups. The latter were asked to consider specific aspects of the problems under consideration and, in particular, to: (a) review and comment on existing assessment methodology, (b) make specific recommendations for the improvement of assessment measurements — particularly of lampreys and prey fish, and (c) itemize and comment on promising, but not yet proven, new ideas on which further research effort should be expended.

There are, of course, available in the literature many good reviews of the methodology of fish stock assessment. The purpose of the present study was to relate available and potential methodology to the existing and future requirements of the sea lamprey control program of the Great Lakes Fishery Commission. For the Task Force to do this properly, it was necessary to consider not only the lamprey, its prey, and their interrelations, but also relevant aspects of the remainder of the fish community and of the background environment of the Great Lakes themselves. In the course of its review, the Task Force took full account of the many relevant points of interest which have arisen during the Sea Lamprey International Symposium.

One of the initial considerations of the Task Force was the question of how feasible was a single management policy for all the Great Lakes. It was accepted that for biological, political, and administrative reasons the fishery management objectives are likely to be different for each lake. However, a clear definition of these objectives is desirable and could be an important part of the strategic planning document at present being discussed by the Great Lakes Fishery Commission.

Lampreys

AVAILABLE SAMPLING METHODS

Ammocoete larvae — Bottom sampling by hand digging or dredge; electric shockers on a CPE basis; use of chemicals (bottom release toxicants); power plant intake screens.

Transformers — Electric shockers; fyke nets; downstream traps; recovery by nets during chemical treatments; power plant intake screens.

Parasitic-phase animals — Direct methods — Animals from commercial fishermen (gill and trap net fisheries); trawling on a CPE basis.

Indirect methods — Attack marks on fish.

Spawning-run adults — Direct methods — Electrical/mechanical barriers; specialized traps (metal, basket type, or inclined plane); dipnet fishery.

Indirect methods — Nest counts; attack marks on fish (using standardized attack mark nomenclature).

ASSESSMENT RECOMMENDATIONS

There should be developed a single improved program for the classification of the Great Lakes tributaries according to their potential for larval lamprey production. This should include quantification of larval and spawning habitat, and the potential for growth rates. Standardized larval assessment techniques based on index stations, CPE techniques, or other agreed methods should be used to quantify the potential contribution to the lake stock thereby indicating priorities for treatment. A technical committee should be established to agree on the details of such a program.

The quality of lamprey attack data should be improved, for it is imperative that attack mark frequencies and other observations on lamprey–fish interactions be continued. As well as an improvement in the level of fish stock assessment (see below), a standard nomenclature for sea lamprey attack marks should be used throughout all projects and should follow the recommendations given by King (1980).

The collection of spawning-run adults by means of standardized portable traps should be continued in all lakes for at least the next 5 years. After this, samples within a lake basin should be taken on a statistically designed basis, though more intensive collecting may have to be initiated in problem areas to evaluate critical situations. The long-term data set on biological and physical characteristics of adult lampreys (sex ratio, length, and weight) should be continued based on the samples obtained in these traps.

RESEARCH RECOMMENDATIONS

The logistics of an adult male lamprey sterilization program should be studied carefully. Important factors for consideration are the ability to capture a large number of males, and (depending on the extent of the program required) the transport, sterilization, and distribution facilities necessary for a practical program.

Research in the field of lamprey attractants and repellents should be encouraged to enhance the control program.

Increased knowledge is required of the parasitic phase of the life cycle of the sea lamprey. Specific information is needed on growth rate, frequency of attack, preferred hosts, movement, behavior, etc. Mark–recapture studies and the measurement of downstream migrants are likely to be an important part of this work as are experimental studies in the laboratory such as those at present being carried out at Hammond Bay.

Fish

AVAILABLE METHODS

Two types of estimates are used to measure the size of wild fish stocks — absolute abundance and relative abundance. Absolute abundance, which is an estimate of the total number of fish (or subsets — e.g. the number of individuals above a certain size or age) in the population is the most useful type of abundance estimate but is normally too difficult or costly to make. Relative abundance is more easily measured, but naturally only relative changes from year to year can be determined. The quality of both types of estimates is enhanced if the population can be stratified into size (or age) classes.

Absolute abundance — Mark–recapture estimation is one of the most common ways to estimate population sizes, but because of the enormous area of the Great Lakes, this is only practical for stock estimates in small areas of the lakes.

Total counts (estimates) in small areas can be extrapolated to large areas. Examples are the use of trawl catches from a known area, counts of fish at barriers, counts of fish nests, etc.

Acoustic equipment. Sophisticated echo sounders can be used to count numbers of fish and estimates can be partitioned into depth strata and size-groups. Traditional gear such as trawls can be used to calibrate the estimates and to partition them into species.

Catch-per-unit-effort when regressed against cumulative catch will produce an absolute abundance estimate, but its precision requires that a significant portion of the stock be caught and this is generally not practicable.

Yield statistics can be used as estimate of minimum abundance, and when combined with estimates of, or assumptions about, potential yield rates can be used to estimate total abundance.

Relative abundance — Catch-per-unit-effort can be used directly to detect relative changes in abundance. It is most commonly calculated from commercial catch statistics or creel census data, but can also be based on index netting conducted specifically for the purpose.

ASSESSMENT RECOMMENDATIONS

In assessment measurements more emphasis must be given to the precision of the estimate than has been done in the past. Some idea of the precision must be available if reliable comparisons of estimates from place to place or year to year are to be made. In planning new sampling strategies, it is also important to have some idea of the precision of the required estimates so that the program may be planned efficiently.

Where commercial catch statistics are being compared, more effort should be made to standardize the estimates used from jurisdiction to jurisdiction. This means that, except where identical gear has been used, the estimates derived from different gear types must be standardized by using previously derived conversion factors. If these are not available (e.g. where new gear is involved) then experimental work should be carried out with the gears concerned to obtain reliable factors.

Every effort should be made to standardize sampling techniques used by the different agencies to estimate fish stocks in the Great Lakes. Though such standardization may not be an easy process (because of differences in the fish communities among the lakes) in agency funding and resources, in objectives, etc., nevertheless it should be regarded as an important long-term objective if the fish populations in the Great Lakes are going to be monitored accurately.

Where relevant, more attention should be given to the assessment of stocks of fish other than the major prey species (e.g. longnose sucker and white sucker) and these assessments should include data such as wounding rates. Their role may be a major one in relation to the fish community as a whole.

RESEARCH RECOMMENDATIONS

The Great Lakes Fishery Commission should be asked to support an evaluation program involving a regular assessment of an important prey species (e.g. lake trout) in the Great Lakes. Such a program could provide accurate assessment data on both prey and host, and thus be of great value to the control program.

The potential of other methods of stock assessment should be explored, particularly the value of acoustic techniques and counts of fish entrained at power stations.

Background Factors

Many assessment programs have failed because the strategies did not take into account the effect of extreme changes in background factors which were not even being measured. It was thus subsequently impossible to try to relate event and cause. Asssessment programs, such as those being carried out on the Great Lakes, must, as many of the recent models have shown, be long-term and more or less continuous to be of value — they are thus likely to span periods of environmental change. The main factors concerned are listed below.

a) Climatic changes, including changes in water levels, etc., may affect the populations concerned. Thus Sjoberg (1980) has suggested a relationship between ice cover and river lamprey abundance in Europe.

b) The pollution abatement program on the Great Lakes will improve many habitats for lamprey and hosts (e.g. as has already happened in the Peshtigo River system).

c) Changes in fishing technology have been discussed above. It is essential that such changes are properly documented in order that the catch efficiency of all gears may be assessed for calibration purposes.

d) The introduction of further exotic fish or the development of fish ranching or cage aquaculture (depending on the species involved) must be viewed with caution. The policy with regard to exotic species should be made clear in the strategic planning document.

e) Changes in catchment land use (e.g. in agriculture and forestry) and in industry (e.g. the combination of more electricity generating stations) are likely to have significant effects on the Great Lakes and their fisheries.

f) The regular use of lampricides in streams is having definite short-term, and possibly long-term, effects on the invertebrate fauna there. There seems to be insufficient information on this topic.

ASSESSMENT RECOMMENDATIONS

It is likely that most of the above background factors are already being monitored by various agencies. It should be confirmed that this is the case and any such monitoring encouraged by the Great Lakes Fishery Commission.

RESEARCH RECOMMENDATIONS

Research on the impact of lampricides on stream and lake zoobenthos and nontarget fish populations should be expanded.

The Future of Sea Lamprey Control

There can be no doubt that the present program of sea lamprey control is a successful one in terms of greatly reducing the populations of sea lamprey in the Great Lakes. However, there is little evidence that it is having any permanent effect on the lamprey and chemical treatments must continue until such time as this is evident or some alternative method of control is found.

The present control program could be enhanced in some measure by:
a) continuing to integrate the Canadian and U.S. programs as closely as possible, especially in terms of assessment methodology and priorities;
b) streamlining the program so that effort at present utilized in some areas could be used to intensify control in areas of high priority; and
c) the development of additional control procedures, e.g. attractants and repellents, male sterilization, etc.

Combined with, and complementary to, the continuing control of the sea lamprey is the question of the rehabilitation of fish stocks in the Great Lakes by continued stocking of appropriate species until natural recruitment appears to be adequate. There is some evidence that the present program may eventually be successful.

The continued use of chemical control is generally regarded as being undesirable ecologically and ideally a stable relationship may develop between lamprey and host populations as in some other lakes. However, this may never happen and continuing research should be carried out to provide an ecologically satisfactory method of controlling the sea lamprey. Many potential ideas for this have been generated by this Symposium and some are worthy of future investigation.

The overall efficacy of control could be enhanced through the establishment of an international control force responsible to the Great Lakes Fishery Commission or its designated committee. Uniform philosophy of treatment would certainly result but, possibly more important, the administrative flow would undoubtedly be more streamlined and probably more cost effective.

Other Proposals

During the meetings of the Task Force a number of relevant topics were discussed which are not included above. The more important ideas are itemized briefly below: some of them at least clearly merit further consideration of research in relation to sea lamprey control in the Great Lakes.

CONTROL METHODS

Physical — 1) Alter the suitability of favorable lamprey spawning sites by the use of baffle fences to reduce flow or by modifying the current or stream bed in some other way.

2) Manipulate the stream temperature in important larval stretches to slow growth and thus increase the spread of treatment. It has been suggested at SLIS that this is occurring naturally in many areas by forest regeneration and subsequent shading (and cooling) of streams.

3) Increase the use of specialized barrier dams and traps — especially those effective for downstream migrants.

Chemical — 1) Increase the acidity of those stretches of stream with the most favorable larval habitat.

2) Establish a chemical method of controlling lamprey spawning.

Biological — 1) Add large numbers of larvae of native nonparasitic species to increase larval population density and so stress resident populations.

2) Determine the mechanism for sex manifestation, to induce the establishment of unisexual populations, preferably of males, through the administration of the proper hormones at appropriate stages.

3a) Establish the mechanism for the initiation of the sex drive in males, and a means of controlling it. 3b) Determine how to control the maturation of gametes through the manipulation of hormones. 3c) Create aggressively spawning sterile males (through 3a and 3b) and release them into streams.

4) Determine the role of the autonomic system in gamete maturation (e.g. by using sympatheticomimetic/parasympatheticomimetic drugs).

HOST–PARASITE RELATIONS

More information is needed on what is the best time of year to collect wound data. Such a study should be carried out in an area where lampreys are reasonably abundant. Host species should be collected at close time intervals and all wounds counted, measured, and aged.

Surveys of wounding rates on species other than lake trout might improve estimates of trends in sea lamprey abundance. Species included could be longnose sucker, white sucker, and rainbow trout.

More effort should be expanded in laboratory studies of the host–parasite relationship, and in particular between the loss of condition and mortality of hosts of different sizes under attack by lampreys of different sizes. Work of this nature has been initiated at the Hammond Bay Biological Station.

ECONOMIC VALUE

The sea lamprey (*Petromyzon marinus*) is still a commercial species in some parts of southern Europe, as is the European river lamprey (*Lampetra fluviatilis*) in the Baltic area. The arctic lamprey (*Lethenteron japonicum*) is economically important in Japan and some parts of the USSR. There seems no reason to suppose that a useful industry for the sea lamprey could not be developed in North America.

Where large numbers of ammocoetes are being caught they could perhaps be sold as bait or used as food in fish farms.

KING, E. L. JR. 1980. Classification of sea lamprey (*Petromyzon marinus*) attack marks on Great Lakes lake trout (*Salvelinus namaycush*). Can. J. Fish. Aquat. Sci. 37: 1989–2006.

SJÖBERG, K. 1980. Ecology of European river lamprey (*Lampetra fluviatilis*) in northern Sweden. Can. J. Fish. Aquat. Sci. 37: 1974–1980.

A Synthesis of Knowns, Unknowns, and Policy Recommendations from the Sea Lamprey International Symposium[1]

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WALTERS, C. J., G. SPANGLER, W. J. CHRISTIE, P. J. MANION, AND J. F. KITCHELL. 1980. A synthesis of knowns, unknowns, and policy recommendations from the Sea Lamprey International Symposium. Can. J. Fish. Aquat. Sci. 37: 2202–2208.

The Sea Lamprey International Symposium (SLIS) has provided a broad spectrum of facts and speculations for consideration in future research and management programs. Many aspects of the laboratory biology and field life history of the sea lamprey (*Petromyzon marinus*) are now well understood. There is little question that it can now be controlled by chemical larvicides, and perhaps in the future by more efficient integrated control programs. There is correlative evidence (wounds, scars, catch curves) that lamprey caused major mortalities in some fish species, and that control in conjunction with stocking has lead to remarkable recoveries of salmonid stocks in the Great Lakes. However, there are great gaps in understanding about just what the lamprey does under field conditions, and it is not yet possible to reject several hypotheses that assign lamprey a minimum or transient role in fish stock changes. Further studies on details of lamprey biology are, in themselves, unlikely to fill the gaps; one alternative is to conduct a large-scale field experiment involving cessation of lamprey control while holding other factors (fishing, stocking) as steady as possible. If it is decided to proceed with management on the assumption that lamprey are important, without the major field experiments to confirm it, then at least the following steps should be taken: (1) the chemical treatment program should be reviewed in detail, with a view to finding treatment schedules that will minimize frequency and dose rates for lampricide applications; (2) pilot studies on alternative control schemes (sterile male, attractants, barriers) should only be funded if they are statistically well designed (several replicate and control streams), and involve quantitative monitoring of lamprey spawning success and subsequent total production of transforming larvae; (3) the lake trout (*Salvelinus namaycush*) stocking program should be maintained at its present level, and should involve diverse genotypes rather than a few hatchery strains; (4) growth in the sport fisheries for lake trout should be curtailed, and commercial fisheries should not yet be permitted; (5) a multispecies harvesting policy should be designed that takes into account the buffering effect of each species on lamprey mortality suffered by others (i.e. should some species not be harvested at all, and viewed instead as buffers for more valuable species?); and (6) a program should be developed for restoring, by culture if necessary, native forage species in case the introduced smelt and alewife should collapse under pressure from fishing and predation by the growing salmonid community.

Key words: sea lamprey, proposed research, fishery management, mathematical models, population dynamics

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WALTERS, C. J., G. SPANGLER, W. J. CHRISTIE, P. J. MANION, AND J. F. KITCHELL. 1980. A synthesis of knowns, unknowns, and policy recommendations from the Sea Lamprey International Symposium. Can. J. Fish. Aquat. Sci. 37: 2202–2208.

Un large éventail de faits et de conjectures ont été présentés au Colloque international sur la grande lamproie marine (SLIS), dont on devra tenir compte dans les futurs programmes de recherche et de gestion. Plusieurs aspects de la biologie de la grande lamproie marine (*Petromyzon marinus*) en laboratoire et de son cycle vital dans la nature sont maintenant bien compris. On peut, bien sûr, contrôler présentement l'espèce au moyen de larvicides chimiques et, plus tard, peut-être par un programme intégré plus efficace. On a des preuves (blessures, cicatrices, courbes de capture) que la lamproie a causé d'importantes mortalités chez certaines espèces de poissons et que son contrôle, conjointement avec un programme d'ensemencement, a résulté en un remarquable rétablissement des stocks de salmonidés dans les Grands Lacs. On est cependant encore loin de comprendre exactement le comportement de la grande lamproie marine dans des conditions naturelles, et on ne peut encore rejeter plusieurs hypothèses à l'effet que l'espèce joue un rôle mineur ou transitoire dans les changements que subissent les stocks de poissons. Il est peu probable que des études plus poussées sur la biologie de la lamproie puissent, par elles-mêmes, combler ces lacunes; une autre approche serait de poursuivre sur le terrain une expérience à haute échelle comportant un arrêt du contrôle de la lamproie, tout en maintenant les autres facteurs (pêche, ensemencement) aussi uniformes que possible. Si l'on décidait de fonder la gestion sur l'hypothèse que la lamproie est importante, sans poursuivre une expérience sur le terrain pour le confirmer, on devrait au moins adopter les mesures suivantes : (1) réexaminer en détail le programme de traitement chimique en vue de mettre en place des programmes qui réduiraient au minimum la fréquence et le dosage des applications de lampricides; (2) ne financer les études pilotes sur d'autres méthodes de contrôle (mâles stériles, substances attractives, barrières) que lorsqu'elles sont bien conçues au point de vue statistique (répétitions et cours d'eau témoins) et comportent l'observation suivie et quantitative du succès de la reproduction des lamproies et la production totale de larves se métamorphosant qui en résulte; (3) maintenir à son niveau actuel l'ensemencement de touladis et utiliser une diversité de génotypes plutôt que quelques lignées de pisciculture; (4) mettre un frein à l'expansion de la pêche sportive du touladi et continuer d'interdire sa pêche commerciale; (5) élaborer une politique de récolte multispécifique, en tenant compte de l'effet tampon de chaque espèce sur la mortalité d'autres espèces, causée par la lamproie (i.e. devrait-on s'abstenir de récolter certaines espèces et les considérer plutôt comme tampons protégeant les espèces plus recherchées ?); et (6) mettre sur pied un programme visant à rétablir, par élevage si nécessaire, les espèces fourrages indigènes, au cas où l'éperlan arc-en-ciel et le gaspareau venaient à manquer sous l'effet de la pêche et de la prédation par une communauté croissante de salmonidés.

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SEA lamprey (*Petromyzon marinus*) control and salmonid stocking programs in the Great Lakes are emerging as one of the great success stories in modern applied ecology. For an investment of roughly $25 million per year, the public is enjoying a fishery worth perhaps 20 times that much. Lamprey are down to 5–10% of their peak abundance, and much has been learned about their basic biology. Mortality rates in lake trout (*Salvelinus namaycush*) have dropped dramatically, and other species have responded as well. While the native fish communities of the Great Lakes can never be restored completely, it now appears feasible to maintain a rich and productive association of species. There remain key uncertainties, and some old problems (mainly unregulated fishery growth) are reappearing, but these all seem small in comparison to what has already been accomplished.

This summary will highlight some of the knowns about lamprey biology and impacts as presented at SLIS, review major uncertainties that remain, and conclude with a discussion of future policies for Great Lakes management. It is written from a critical point of view; we hope to be constructive, and we do not mean to minimize the profound accomplishments of the people who made it all happen in the first place. Source documents for this summary include the technical papers published in this volume together with the reports of the three task forces who met during the symposium. Task forces served as abstractors and synthesizers of information relevant to the topics of: (1) stock effects, i.e. those phenomena related to predator/prey ratios; (2) control theory, dealing with the regulation of lamprey numbers; and (3) assessment measurements which enable us to understand the present status of the Great Lake fish communities. Our synthesis avoids specific citation of these reports and earlier published accounts; it is the product of the conspicuous interactions that occurred among symposium participants. We remain, of course, solely responsible for any gross distortions of fact or misinterpretation contained herein.

Some Confident Observations

The knowns about Great Lakes sea lamprey fall into three areas: basic biology, life history in response to control measures, and correlations with changes in fish stocks. It would be inappropriate here to itemize the details presented at SLIS about lamprey anatomy, physiology, and behavior. This information has been and will continue to be essential in developing and interpreting various control tactics (i.e. 3-trifluoromethyl-4-nitrophenol (TFM) is inactivated by glucoronyl transferase in teleost livers, but not in lamprey). Of particular value will be observations about maturation and spawning behavior (in relation to sterile male programs), responses to chemical attractants, and larval development in relation to habitat factors such as temperature. The emphasis below will be on observations that relate to the lamprey's overall population dynamics and pest status.

LAMPREY LIFE HISTORY AND POPULATION DYNAMICS

Perhaps the most striking features of the lamprey's biology are its abilities to disperse into new habitats and to increase explosively in abundance. It spread through the Great Lakes as a hitchhiker on boats and mobile prey, and invaded hundreds of streams along the way. In lakes Huron, Michigan, and Superior, it reached peak abundance about 20 yr after first being reported. Assuming a life cycle of roughly 7 yr and conservative estimates of ¼ million spawners per lake at the peaks, the lamprey must have increased 20- to 50-fold per generation. Considering fecundity estimates (roughly 60 000 eggs/ ♀) presented at SLIS, this rate of population increase could be accomplished with only a 10% egg survival rate, 10% survival of larvae to transformation, and 20% survival through the parasitic stage.

Many aspects of lamprey reproduction are well understood. The size and fecundity of lamprey spawners depends on the abundance and sizes of prey available, but the fecundity is impressive in any case. Since chemical treatment began, sex ratios have shifted toward females (sex determination mechanisms not understood), exaggerating effects of prey population recovery on total fecundity. Lamprey require unpolluted streams for successful spawning, and pollution abatement programs are creating new lamprey habitat and subsequent problems for the lamprey control agents. There has been some concern that chemical treatment of streams will result in selection for resistant or lake spawning lamprey strains. Larvae are now found in littoral areas off stream mouths, but these larvae might just be dispersers from stream spawning.

Hatching larvae drift downstream from spawning sites and usually establish burrows within a short distance. The average size (and apparently age) of larvae increases downstream from spawning areas. The larvae are filter feeders on apparently abundant detrital resources, though they show density-related changes in average growth rate. The size at transformation (to parasitic, lake feeding stage) is similar in different habitats with larvae taking longer to reach this size in poor (crowded, low temperature, etc.) than in good habitats. While a few larvae may metamorphose at age three, most apparently require at least 5 yr in good habitats and even longer in poor ones. Transformed lamprey migrate downstream mainly in late fall and winter, while spawning is in spring. This means that fall chemical treatments will catch an extra year-class in comparison to spring treatments. Some streams have been treated every 3 yr, and data presented at SLIS indicate that this is generally unnecessary.

INTERACTIONS WITH PREY

Parasitic stage lampreys can disperse quite widely, and changes in spatial distribution are related mostly to prey movements. Potential impact on prey increases through the first summer and fall of lake residence, as the lamprey grow and feed actively in warmer waters (10–15°C). Feeding rates drop off in winter, and there is little feeding the following spring before they mature and spawn. In laboratory studies they feed mainly on blood (not other tissues), and select the largest prey available; about half the attacks result in death of the prey. Larger prey individuals are more likely to survive attacks. There is no direct evidence on the percentage of attacks that result in prey deaths in the field. Lamprey in the laboratory may remain attached to each prey (and therefore be unavailable to attack others) for times ranging from a few hours to several weeks.

RESPONSE TO TREATMENT

Early efforts at lamprey control (involving mechanical and electrical barriers) were not fully effective, apparently because of the difficulty in maintaining the units in continuous, uninterrupted operation through consecutive migratory seasons. The chemical treatment program was immediately and dramatically successful; lamprey disappeared entirely from many streams, and others had so few spawners that resulting larval production was comparatively low. However, there remain a few troublesome water systems (i.e. St. Mary's River) that have not been treated for various tactical reasons. Lamprey from these systems, plus residuals from chemical treatment, continue to result in relative abundances (spawning counts at index barriers) about 5–10% of historical peaks. There is no evidence as yet of genetic strains resistant to TFM treatment.

IMPACTS ON PREY SPECIES

The impact of lamprey on prey populations has not been measured directly in the field. Rather, it has been inferred from correlations among (1) lamprey abundance and prey abundance and size distribution; (2) lamprey abundance and total prey mortality rates estimated by tagging and catch curves; and (3) lamprey wounding/scarring rates and total prey mortality rates. Declines in lake trout and whitefish abundance coincided in the upper Great Lakes with appearance of lamprey; stocking programs were generally unsuccessful until after control had radically reduced lamprey numbers. Total mortality rates declined following lamprey control, but with a lag of several years. Mortality rates and wounding/scarring rates have been well correlated, but the Cayuga Lake studies show that such correlations can be spurious.

The laboratory and field data covering lamprey impacts are in general agreement with one another, as evidenced by the lake trout simulation model produced for SLIS. When laboratory estimates of prey consumption per lamprey are combined with field data on lamprey abundance and on mortality rates due to fishing, resulting estimates of total mortality (for Lake Superior) are consistent with field estimates. The model produces response lags as observed, and attributes these to the combined effect of stocking and lamprey control on the predator:prey ratio. However, the model predicts much higher mortality rates in Cayuga Lake than have been observed.

Synthesis Models

Each researcher and manager at SLIS came armed with an array of data, concepts, predictions, and priorities. Each carried a relatively refined mental model for his area of specialization, and usually some very simplistic model of how "the rest of the system" works. Unfortunately, the soundness of his recommendations for future activity is dependent on both models, with the weaker acting as a kind of logical limiting factor. For example, a lamprey specialist may be fully familiar with the impacts on ammocoetes of various control policies, yet assume that proportionately fewer lamprey just means proportionately more fish. His arguments about the value of control to fisheries are questionable, since the fish response is unlikely to be simple proportionality.

The integration or synthesis of specialized viewpoints demands some device for logically connecting the refined models, while discarding or minimizing the number of weak arguments. A modeling group attempted to develop quantitative dynamic models as "deductive engines" to integrate a few of the specialized views that emerged most prominently at SLIS. This group did not try to obtain the "whole picture" (it does not exist anyway, since every model is connected into some larger system about which we still have to be simplistic), and had to rely on personal judgments about which specializations to include and about what constitutes the "soundest" of refined models. Their conclusions may be totally incorrect; they can only claim to have examined the problem from a slightly broader viewpoint than the specialists who provided the pieces.

The models were discussed with and demonstrated to many specialists at SLIS. They evolved considerably through this process, and now appear to give quite credible predictions considering that they are generally based on very simple assumptions and sheer guesses at many quantitative parameters. They helped to resolve some specific policy questions, but the formulation of them served a more useful purpose by helping to clarify what more should be learned about the system.

Glaring Gaps and Alternative Hypotheses

There are large gaps in understanding about lamprey responses under natural conditions. The uncertainties fall in three main areas: (1) regulation of numbers in the absence of control measures; (2) importance of alternative sources of animals that repopulate streams after chemical control; and (3) parasitic feeding behavior and impacts on prey. These areas lie at an intermediate level of ecological description, where observation and experimentation are most difficult. They will not be fully resolved by doing more detailed studies on organisms isolated from natural environments, since they may involve behavioral and physiological processes that are never expressed in the restricted arenas of experimental biology (also, there are too many details to study). Also the answers will not likely emerge from longer time series of monitoring data on overall system behavior, since nature will probably not produce the necessary contrasts in possible causal factors.

LAMPREY POPULATION REGULATION

Considering the high rates of egg and larval production by lampreys, the concensus at SLIS was that natural population regulation must occur either through (1) stream habitat limits on production of transformed larvae, or (2) changes in parasitic stage survival associated with reduced prey abundance at high lamprey densities. The stream habitat hypotheses have implications for lamprey control as well, since measures to reduce spawning (sterile males releases, barriers, and weirs) will be ineffective unless spawning is reduced enough so that larval survival will not be enhanced through further reductions in larval density.

Several specific hypotheses were proposed as to how larval density regulation might be accomplished. Larvae with established burrows might release chemical repellents that prevent further settling; local food competition may lead to reduced growth and later transformation, and therefore to lower overall survival. Unfortunately, general observations have not even been assembled on the "stock–recruit" relationship between egg deposition and resulting transformer production.

This is understandable considering that no accurate technique for aging transformers has been found. Also the control agents have not left any accessable, researchable streams as untreated study areas; the costs of such studies would have to include possible losses of fish production due to allowing extra lamprey into the lakes, plus increased costs of control in nearby streams to which adults from the study areas might disperse.

There are two types of correlative evidence that prey abundance may limit lamprey numbers. First, body sizes of spawning lampreys are related to indices of prey abundance. However, it has not been shown that survival of parasitic lamprey is related to growth rate, and even small adults have imposing fecundities. Second, lamprey declines have followed the collapse of lake trout in each of the upper lakes. However, these declines also coincide with the onset of intensive control measures. Lamprey numbers have not responded to recent increases in prey abundance, but one could argue that this is due to improved efficiency of chemical control.

LAMPREY DISPERSAL

Streams are often repopulated immediately after chemical control, so retreatment becomes necessary within a few years. There are two possible sources of repopulating spawners: survivors from treatment, and colonizers from areas that have not been treated for various reasons. It could well be that the colonizer component is large enough in many streams to render controls on spawning success (sterile male releases, etc.) and other nonlampricide treatments ineffective. There may always be enough spawners to saturate larval rearing environments. Thus the success of integrated control programs may depend on large investments to treat the problem streams. Also, the presence of colonizers may confound attempts to measure performance of chemical treatment in terms of survivors that return to spawn; chemical treatment may be even more effective than has been suspected, and it might be possible to reduce dose rates and treatment frequencies dramatically just by hitting a few problem streams very hard.

PREDATOR–PREY INTERACTIONS

There are three major unknowns about the impact of lampreys in the field: (1) the effect of prey density on number of attacks per lamprey (i.e. do lampreys spend a large percentage of their time searching or waiting for prey?); (2) the attachment and subsequent nonreactive time per attack (how many attacks can an individual lamprey make?); and (3) the proportion of attacks that result in prey deaths. Even gross, average values of these variables would be helpful in assessing lamprey impacts, though obviously it would be better to know them as functions of season, lamprey size, and prey size and species.

For simple impact estimates involving rehabilitated prey stocks, prey density effects can probably be ignored. That is, lamprey searching times will be short and the number of attacks will be limited mainly by the attachment time per attack. Assessments based on this simplification would in effect be assuming that lamprey are a depensatory mortality agent, with all the dangers that such agents imply in calculations about prey population dynamics.

The total time per attack (attachment plus subsequent nonreactive time) is another matter. This time sets the ultimate limit on lamprey predation rates, and determines the extent to which any one prey acts to "buffer" other prey against attack. Arguments about reducing lamprey impacts by decreasing the predator:prey ratio are meaningless if the normal (field) times per attack are small, as are arguments about increasing the number of large prey individuals (i.e. by reducing lake trout harvest rates) as a means to buffer smaller individuals against attack.

Finally, uncertainty about the probability of death per attack makes it impossible to infer death rates from wounding/scarring data, and leaves open the whole question of whether lamprey are predators or benign parasites. Several hypotheses were presented at SLIS as to why lampreys might have evolved to kill far fewer prey in the field than they do under laboratory conditions. They may attain higher average rations by leaving each prey long before "sucking it dry." They may leave each prey before weakening it so much that it drops out of its school or aggregation, thus separating them from a ready source of hosts. They may conduct more nonfeeding or slow feeding attachments in the field, simply as a means to disperse or migrate. A disturbing possibility is that lamprey can somehow perceive or measure prey densities; they may then act as benign parasites when prey densities are high, but become more tenacious (i.e. predators) when prey are scarce.

Vampires in the Basement, or Skeletons in the Closet?

As delightfully expressed by Jim Kitchell, the prevailing belief at SLIS is that the lamprey problem is like having vampires in the basement; if the door is ever opened there will be deep trouble indeed. But the uncertainties outlined above make it impossible to reject conclusively several general hypotheses that argue against continuing intensive lamprey control. These hypotheses will come back to haunt the control program in its dealings with environmental groups and funding agencies. The cheapest long run solution may be to resolve them once and for all by temporarily (10–15 yr) stopping lamprey control on one of the Great Lakes, while maintaining other factors (fishing, stocking) as constant as possible.

One possibility is that lamprey never were a serious problem, except perhaps to help initiate stock collapses that would eventually have occurred anyway as a result of overfishing. The various extinctions may have been caused by whatever unknown agent(s) are preventing successful lake trout spawning now in Lake Michigan and parts of Lake Superior. Laboratory data uniformly argue against this hypothesis, as do mortality studies on fish planted during years of peak lamprey abundance. However, the Cayuga Lake data appear to support it.

A second hypothesis is that lamprey are a depensatory mortality agent (i.e. caused extinctions but did not trigger declines) and are not a danger when prey densities are high; the way to manage the system is by heavy stocking and/or restricted fishing. The SLIS lake trout/lamprey simulation model argues against this hypothesis; it indicates that lamprey abundance of only one third the historical peak would be sufficient to cause another collapse even in the absence of fishing. However, that model is based again on laboratory estimates of trout mortality per lamprey.

A third possibility is that abundance of feeding lamprey would naturally be limited at far below historical peaks by density-dependent processes acting to reduce transformation rates of larvae. The SLIS lamprey dynamics model produces an effect like this (abundance peak followed by lower equilibrium), but predicts that the equilibrium could still be devastatingly high. It would take 15–20 yr to resolve the question by following transformer outputs and spawner abundance in several streams after stopping control on them.

A final possibility is that cessation of lamprey control would lead to a "predator–prey balance" with lamprey abundance limited by availability of fish prey, yet with valuable prey species (lake trout, etc.) still acceptably numerous. Strong natural selection might soon result in fish strains able to withstand or avoid lamprey. Unfortunately for this idea, it is even more likely that less valued fish species would support a high enough abundance of lamprey to reduce substantially the valuable species just through chance encounters.

Policy Recommendations

The existence of large uncertainties implies that the sea lamprey control program should not be considered a simple problem of optimizing the allocation of resources toward some desired objective (i.e. minimizing lamprey to allow more fish production). Rather, the program should be treated as a grand gamble, with odds that are difficult to calculate objectively. A gambler would ask some questions that are not usually raised by resource management planners. How much is it worth investing in lamprey control just as insurance against the risk of another fishery collapse, not even pretending that such a collapse would necessarily occur without control? Should governments pay for this insurance policy? How much would it be worth to know for sure that control is not necessary, and is there a way to pay this "price of information" without incurring unacceptable risks; more precisely, is it worth risking another collapse in one Great Lake just to prove that control is still necessary in the others, or is there a smaller field arena (such as a large bay) that is worth risking? How should potential long run dangers, such as escalating control costs due to appearance of resistant lamprey strains, be weighted against the immediate benefits of control? There can be no fully objective "optimal" answer to these questions, since there are no generally acceptable standards of risk aversion or time preference. They are largely political questions, though bounded by scientific and technological constraints, and should be debated as such.

It seems likely that intensive lamprey control will be continued, and many recommendations were voiced at SLIS as to how it might be improved and related to other fisheries management activities. The following is an attempt to summarize briefly these recommendations.

1. Take Steps to Improve the Chemical Treatment Program

Chemical treatment is unlikely to eradicate the lamprey entirely, so that there is no point in trying to eliminate every last larva from treatable streams. Treatment frequencies and dose rates should be reduced, and better use made of habitat classification information so as to treat streams no more often than is necessary, based on expected larval development times. Critical treatments should be concentrated in the fall wherever feasable.

2. Require Statistically Sound Designs and Intensive Monitoring Schemes for Pilot Experiments Involving Alternative Treatment Techniques

The history of Great Lakes management is a comedy of confounded factors and ambiguous monitoring programs. It is time to stop pretending that expedient management justifies or requires cutting some corners scientifically. Each pilot control scheme should be replicated in several streams, with several nearby streams as controls. Spawning numbers and total transformer production should be monitored for at least 10 yr in all of them. If all this appears to be too costly, consider trying fewer alternatives. Consider the costs of widely applying a management scheme derived from a poorly designed pilot study, which in fact had no real effect.

3. Develop an Intensive Study of Streams Colonized by Lampreys Following Pollution Abatement

Water-quality legislation enacted recently and enforced in the near future will assure reoccurrence of the Peshtigo River case history. If properly anticipated, monitored, and replicated elsewhere, streams recently colonized by lamprey offer experimental study sites of lamprey biology (e.g. colonizing rates, ammocoete growth rate and carrying capacity, etc.) applicable in general and in the development of management strategies for these kinds of habitats which will very probably become a major concern of the control agents.

4. Invest in a Search for "Natural" Lamprey Controls

Studies should be funded on the biology of natural lamprey populations on the Atlantic coast, and on Great Lakes streams that have never been successfully invaded by the sea lamprey. It would be equally valuable to know how natural, coevolved, lamprey/prey associations differ from the Great Lakes situation. Also, dispersal and colonization mechanisms are poorly understood, but may hold the key to control measures that capitalize upon natural attractants produced by ammocoetes.

5. Conduct Large-Scale Experiments on the Effects of Reduced Lamprey Control and Overfishing

Lamprey control should be stopped, or chemical treatments greatly reduced, in a restricted area of the Great Lakes. Fishing rates that are thought to be excessive for lake trout should be permitted in another area.

6. Review and Revise Salmonid Stocking Programs

Salmonid stocking rates should not be increased rapidly, because of the risk of causing a collapse of introduced forage fish. Lake trout stocking rates should be held steady to facilitate monitoring of natural population recovery, and efforts should be made to diversify the genetic strains used for stocking.

7. Restrict Exploitation Rates on Lake Trout

The salmonid sport fisheries are growing rapidly, and involve efficient new technologies; there is demand to reinstate commercial fishing. The lamprey is still abundant enough to cause considerable mortalities, especially if prey stocks are reduced. Thus the stage is set for a repeat of the historical collapses, or at least prevention of native stock recovery.

8. Develop an Overall Fishing Policy for Species Impacted by Lamprey Predation

Major decreases in any prey stocks may result in more lamprey attacks on other stocks; stocks are now interdependent through mutual buffering of lamprey predation. Enough data are available to permit rough calculation of at least a few key trade-offs (i.e. increase in lake trout mortality and decrease in potential yield due to increased whitefish harvest) and associated changes in overall fishery value. It may well turn out that some species should not be harvested at all, at least until others have had more time to recover.

9. Develop a Rehabilitation Program for Native Forage Species

Native forage species for salmonids appear to be recovering (at least in Lake Michigan), perhaps as a result of reductions in introduced species (smelt, alewife) by salmonid predation and fishing. This recovery might be hastened by culture programs, and should ultimately result in a more stable predator/prey association since the native species are better adapted to salmonid predation.

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COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

Digestibilité chez la Truite arc-en-ciel (*Salmo gairdneri*) lors de l'adaptation à un nouveau régime alimentaire **J. de la Noüe, G. Choubert, B. Pagniez, J. M. Blanc et P. Luquet**

Myxosoma cerebralis: trypsinization of plankton centrifuge harvests increases optical clarity and spore concentration **M. E. Markiw and K. Wolf**

Stable cycles in multistage recruitment models: an application to the Northern California Dungeness crab (*Cancer magister*) fishery **R. McKelvey, D. Hankin, K. Yanosko, and C. Snygg**

Differentiation in *Coregonus zenithicus* in Lake Superior **T. N. Todd and G. R. Smith**

Recurrence of kills of Atlantic herring (*Clupea harengus harengus*) caused by dinoflagellate toxins transferred through herbivorous zooplankton **A. W. White**

Isolation and identification of an atypical *Aeromonas salmonicida* strain causing epizootic losses among Atlantic salmon (*Salmo salar*) reared in a Nova Scotian hatchery **W. D. Paterson, D. Dovey, and D. Desautels**

Seston ecology of the surface waters of Hudson Bay **J. T. Anderson and J. C. Roff**

Using *r-K* selection theory to predict natural mortality **D. R. Gunderson**

Use of a multiplicative model to estimate catch rate and effort from commercial data **S. Gavaris**

Viral erythrocytic necrosis (VEN) in Atlantic cod (*Gadus morhua*): in vitro studies **P. W. Reno and B. L. Nicholson**

Crustacean zooplankton communities of acidic metal-contaminated lakes near Sudbury, Ontario **N. D. Yan and R. Strus**

Variability in the diet of ringed seals, *Phoca hispida*, in Alaska **L. F. Lowry, K. J. Frost, and J. J. Burns**

Differential prey vulnerability and predator selectivity: effects of evasive prey on bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) predation **G. L. Vinyard**

Depression of primary productivity by humic matter in lake and reservoir waters of the boreal forest zone **T. A. Jackson and R. E. Hecky**

Accumulation of benzo[*a*]pyrene in a larval bivalve via trophic transfer **C. J. Dobroski Jr. and C. E. Epifanio**

Notes

Comparison of two methods of estimating the variance of the estimate of catch per unit effort **S. J. Smith**

Origin of a relict population of *Salvelinus* in Bear Creek of the Alsek River drainage, Yukon Territory **C. B. Sikstrom**

Teratogenesis in lake trout (*Salvelinus namaycush*)in an experimentally acidified lake **L. A. Kennedy**

Acoustically derived estimate of the size distribution for a sample of sperm whales (*Physeter catodon*) in the Western North Atlantic **H. S. Adler-Fenchel**

Possible sexing technique for humpback whales (*Megaptera novaeangliae*) **V. P. Jurasz, D. McSweeney, and C. M. Jurasz**

Letters and comments/Lettres et commentaires: Comment on Deriso's delay-difference population model **C. J. Walters**

Book reviews/Comptes rendus: Handbook of phycological methods. Physiological and biochemical methods (J. A. Hellebust and J. S. Craigie [ed.]) **R. A. Chastain and R. A. Lewin**

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